ECOLOGY OF THE BURROWING AMPHIPOD

PONTOPOREIA AFFINIS IN LAKE MCIHIGAN

by

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ABSTRACT

The ecology of the burrowing amphipod

Pontoporeia affinis in Lake Michigan

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Wayne P. Alley

The Great Lakes Research Division of the University of Michigan collected macrobenthos samples and measured environmental parameters at 35 stations in the southern two-thirds of Lake Michigan. The stations of this three year long-term study were sampled monthly in triplicate from August to November 1964, from April to November 1965, and from March to November 1966. Environmental parameters: sediment type, percent carbon in the sediment, water temperature, distance from shore, and depth were chosen as variables likely to affect the abundance and distribution of the macrobenthic biota.

A second study site, called the short-term study area, was located off Mona Lake, Michigan. Eighty-eight samples were collected there 13-14 June 1967 by two divers using a hand coring device.

Physical and biological parameters collected at these two study areas were utilized in studying the ecology of the burrowing amphipod _Pontoporeia affinis_ in Lake Michigan. The patterns of reproduction, changes in seasonal abundance, patterns of spatial distribution, and the

interspecific and intraspecific associations of this amphipod were examined.

The brood chambers of adult female amphipods, collected in the long-term study area, indicated that reproduction is completed by late May-early June at depths less than 35 m and beyond 35 m the amphipod population breeds intermittently throughout our sampling seasons. The fact that adults die after reproduction simplifies the recognition of year classes. Size frequency histograms, collected throughout the sampling seasons, indicated that Pontoporeia living at a depth of 10 m mature in one year, those inhabiting a depth zone of 20-35 m require two years to mature, and those living at depths greater than 35 m possibly require 3 years to mature.

Juvenile Pontoporeia approximately 2 mm long conformed to a normal distribution and juvenile amphipods approximately 7 mm long were randomly distributed at the short-term study area. The two size groups appeared to be positively associated with each other. Both size groups were negatively associated with the oligochaetes, the large size group was negatively associated with the sphaeriids, and no association occurred between amphipods and the chironomids.

Total Pontoporeia of the long-term study area were associated in a positive manner with the oligochaetes, sphaeriids, and chironomids. This positive association is attributable to larger benthos samplers that masked the microassociations of the benthic organisms.

A concentration of _Pontoporeia_ exists around the 35 m depth contour, which usually coincides with the junction of the profundal and sublittoral zones. The low density of amphipods in the sublittoral is due to the environmental extremes of this area, while the profundal has a more uniform environment and fewer amphipods, which is here attributed to a slower growth rate and less available food.

The lake was divided into four depth zones: 10-35 m, 36-65 m, 66-105 m, and greater than 105 m, and the effects of the environment on the abundance of _Pontoporeia_ were examined by stepwise multiple regression analysis for these depth zones. The multiple correlation coefficients for these zones were: 0.756 at 10-35 m, 0.599 at 36-65 m, 0.677 at 66-105 m, and 0.826 at the greater than 105 m depth zone. When all depths were combined the multiple correlation coefficient was 0.796. These high correlation coefficients indicate that the environmental variables statistically contributed a considerable amount of information about changes in amphipod abundance.

The average standing crop of _Pontoporeia_ was examined for the individual depth zones and all depths combined; and, in general, there did not appear to be any major deviations among the average standing crops for the three sampling seasons.

The patterns of seasonal amphipod abundance were examined at six profundal stations of one transect, and these patterns appeared to be quite similar, particularly for adjacent pairs of stations.

The average standing crop of Pontoporeia was estimated for each station of the five transects, and the effect of depth was removed statistically from these data. The results indicated that stations located in regions subjected to upwelling had a larger standing crop of amphipods than other regions in the lake. Stations located in areas where bottom sediments were variable had, on the average, a lower standing crop of amphipods.

INTRODUCTION

The burrowing amphipod Pontoporeia affinis Lindström (1855), the most abundant macrobenthic organism in Lake Michigan, was originally described from lakes in northern Germany. Subsequently, Smith (1874) described P. hoyi and P. filicornis from the Great Lakes. Ekman (1913) described P. weltneri from Lake Vättern, Sweden. Juday and Birge (1927) sent specimens of P. hoyi from Green Lake, Wisconsin, to G. O. Sars who concluded that this species was synonymous with P. affinis. Adamstone (1928) decided that P. filicornis was also identical with P. affinis. Segerstråle (1937, 1950) in a revision of the genus, showed that males of P. affinis and P. welterni were identical and that P. kendalii, described by Norton (1909) from Lake Champlain, Vt., was also synonymous with P. affinis. Bousfield (1958) indicated that a large, ecologically distinct form of this amphipod found in the Ungava Bay region of Quebec may prove to be distinct from the Lindström form. However, Bousfield concluded that the Ungava Bay amphipod should be designated Pontoporeia affinis until more information on the taxonomy, distributional ecology, and physiology of this organism becomes available.

Segerstråle (1937) concluded that P. filicornis is identical with the penultimate instar of P. affinis and suggested that it may be a neotenic form of P. affinis. He designated P. filicornis as P. affinis var. brevicornis. It is interesting to note that while P. affinis var. typica

has been recorded from both European and North American lakes, _P. affinis_ var. _brevicornis_ is found only in North America, which suggests that the latter form developed in this continent since the Pleistocene. Segerstråle (personal communication) has found _brevicornis_ in all the St. Lawrence Great Lakes with the exception of Lake Ontario and feels that it will also be found there with additional sampling.

Segerstråle (1959) presents an excellent account of the distribution of _P. affinis_ in Eurasia, while Henson (1954) gives an extensive review of the North American distribution. _Pontoporeia affinis_ is found in the brackish waters of arctic Russia, Siberia, and Alaska, and within the Baltic and Caspian Seas. It inhabits the oligotrophic lakes of the once glaciated sections of northern Europe and is also widely distributed in Siberian lakes and the estuaries and rivers of arctic Eurasia. In North America it has been reported in the larger oligotrophic lakes of Canada, Ungava Bay, St. Lawrence estuary, the Great Lakes, Green Lake of Wisconsin, the Finger Lakes of New York, and Lake Washington on the west coast.

Various workers have provided estimates of the numerical importance of this amphipod in Lake Michigan. Eggleton (1936, 1937) reported as many as 8,400 individuals/m^2 at one station and showed that this amphipod comprised 64 percent of the total number of macrobenthic invertebrates. An examination of his data indicates an average of approximately 700 amphipods/m^2. Merna (1960) found the average standing

crop of P. affinis in the lake to be approximately 1,700 individuals/m^2, and that 70 percent of the total wet volume of the macrobenthos consisted of Pontoporeia. Henson and Chandler (unpublished data), cited by Henson (1966), found approximately 1,500 individuals/m^2 in the Straits of Mackinac. Marzolf (1965) noted more than 14,000 amphipods/m^2 at one station in the Grand Traverse Bay region. Powers et al. (1967) recorded one station in the lake where P. affinis exceeded 23,000 individuals/m^2. Powers and Alley (1967) showed that the average standing crop of this amphipod exceeded more than 2,700 individuals/m^2 and that it comprised 64 percent of the total macrobenthos. In a comparative study, Robertson and Alley (1966) showed that the average abundance of P. affinis, oligochaetes, and sphaeriids was significantly greater in 1964 than in 1931.

RESEARCH PLAN

With the present interest concerning the rates of eutrophication and increase in pollution, and because this amphipod is the first macrobenthic organism to be driven out by increased pollution, it is reasonable to study it. The objective of this investigation was to gain information on the ecology of the amphipod Pontoporeia affinis in Lake Michigan and to evaluate its normal patterns of reproduction, normal changes in seasonal abundance, and normal patterns of spatial distribution. When these are known, pollution-caused deviations can be recognized.

The data presented here were collected during comprehensive

multidisciplinary studies of Lake Michigan carried out by the Great Lakes Research Division of the University of Michigan. This program represented the first coordinated long-term study of the physical-chemical environment and of the biota of the lake. It provided an abundance of data applicable to problems concerning the annual fluctuations of the biota and to the interrelationships of these organisms with their environment.

These data were collected in two different study areas. The first study area, which is called the long-term study area, consisted of 35 stations located in the southern two-thirds of Lake Michigan (Fig. 1). Thirty-three stations were located on five cross-lake transects. These transects were assigned letter designations, and the stations of each transect were numbered serially from east to west. Stations on transects A, B, and C were positioned according to major surficial bottom sediment types as described by Ayers and Hough (1964). Since detailed information on bottom types was not available for the northern basin, stations on the D and E transects were positioned according to major bathymetric features. The remaining two stations of the long-term study area were located off Muskegon and were designated C'-1 and C'-2. The locations, depths, and sediment types of these 35 stations are presented in Table 1. Sediment-type nomenclature is explained in a subsequent section under "METHODS AND MATERIALS." Sampling was carried out monthly from August to November 1964, from April to

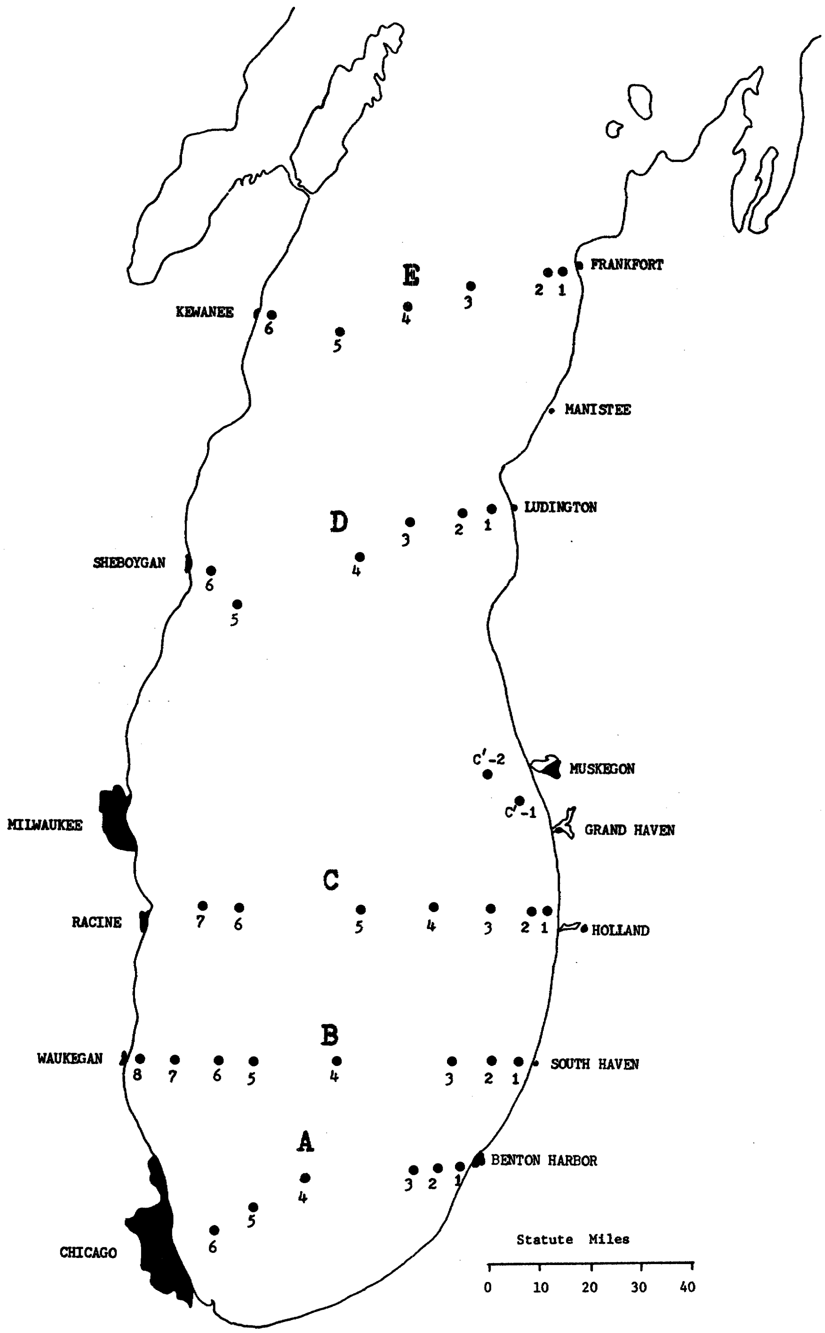

FIG. 1. Index map of the Lake Michigan macrobenthos stations of the long-term study area that were sampled from 1964 to 1966.

November 1965, and from March to November 1966. Stations of the B and D transects were not sampled after June 1966.

Patterns of reproduction of Pontoporeia were studied by examination of brooding and spent females and by analysis of the size frequency of amphipod populations from various depth zones. The environmental parameters, sediment type, percent organic carbon in the sediment, water temperature, distance from shore, wave height, and depth were chosen as environmental factors likely to affect the abundance and distribution of Pontoporeia. These variables were measured and recorded at each benthic sampling station.

The second study area, called the short-term study area, was located near Mona Lake approximately 6,000 feet from shore at a depth of 56 feet (Fig. 2). Eighty-eight benthos samples were collected at two adjacent 15 x 15 ft. areas 13-14 June 1967. These samples were used to determine the small-scale patterns of Pontoporeia distribution and to examine the microassociation of Pontoporeia and the other macrobenthic organisms.

TABLE 1. Location, depth, and sediment type of the Lake Michigan benthos stations.

Station	Location N lat	Location W long	Depth Meters	Sediment Type
A-1	42°06'30"	86°32'00"	18	Sand
A-2	42°06'00"	86°37'00"	35	Silty sand-sandy silt
A-3	42°05'30"	86°43'00"	70	Silt-clayey silt
A-4	42°03'30"	87°06'30"	74	Layered
A-5	41°57'00"	87°18'30"	43	Silty sand; sand and gravel
A-6	41°52'00"	87°27'00"	18	Sand and gravel; gravel
B-1	42°24'00"	86°20'30"	19	Sand
B-2	42°24'00"	86°27'00"	47	Silt-clayey silt
B-3	42°24'00"	86°35'30"	68	Silt-clayey silt
B-4	42°23'30"	87°01'00"	129	Silt-clayey silt
B-5	42°22'30"	87°21'00"	108	Silt-clayey silt
B-6	42°22'30"	87°30'00"	83	Layered
B-7	42°22'00"	87°40'00"	45	Silty sand-sandy silt
B-8	42°22'00"	87°47'30"	11	Sand
C-1	42°49'40"	86°14'50"	20	Sand
C-2	42°49'40"	86°18'25"	50	Silt-clayey silt
C-3	42°49'10"	86°28'25"	77	Silt-clayey silt
C-4	42°48'50"	86°41'30"	108	Layered
C-5	42°49'00"	86°50'00"	157	Silt-clayey silt
C-6	42°47'40"	87°26'50"	99	Layered
C-7	42°47'30"	87°34'30"	55	Silty sand-sandy silt
C'-1	43°08'00"	86°23'00"	38	Silty sand-sandy silt
C'-2	43°12'00"	86°31'00"	93	Silty sand-sandy silt
D-1	43°57'00"	86°33'00"	30	Sand
D-2	43°56'00"	86°39'30"	98	Layered
D-3	43°54'00"	86°51'30"	170	Silt-clayey silt
D-4	43°48'00"	87°03'00"	131	Layered
D-5	43°38'40"	87°31'00"	119	Layered
D-6	43°44'00"	87°38'00"	30	Sand
E-1	44°37'30"	86°18'12"	44	Sand
E-2	44°37'00"	86°21'42"	197	Silt-clayey silt
E-3	44°34'00"	86°40'00"	271	Silt-clayey silt
E-4	44°30'18"	86°55'18"	216	Silt-clayey silt; layered
E-5	44°25'30"	87°10'18"	173	Silt-clayey silt
E-6	44°27'48"	87°26'25"	33	Sand

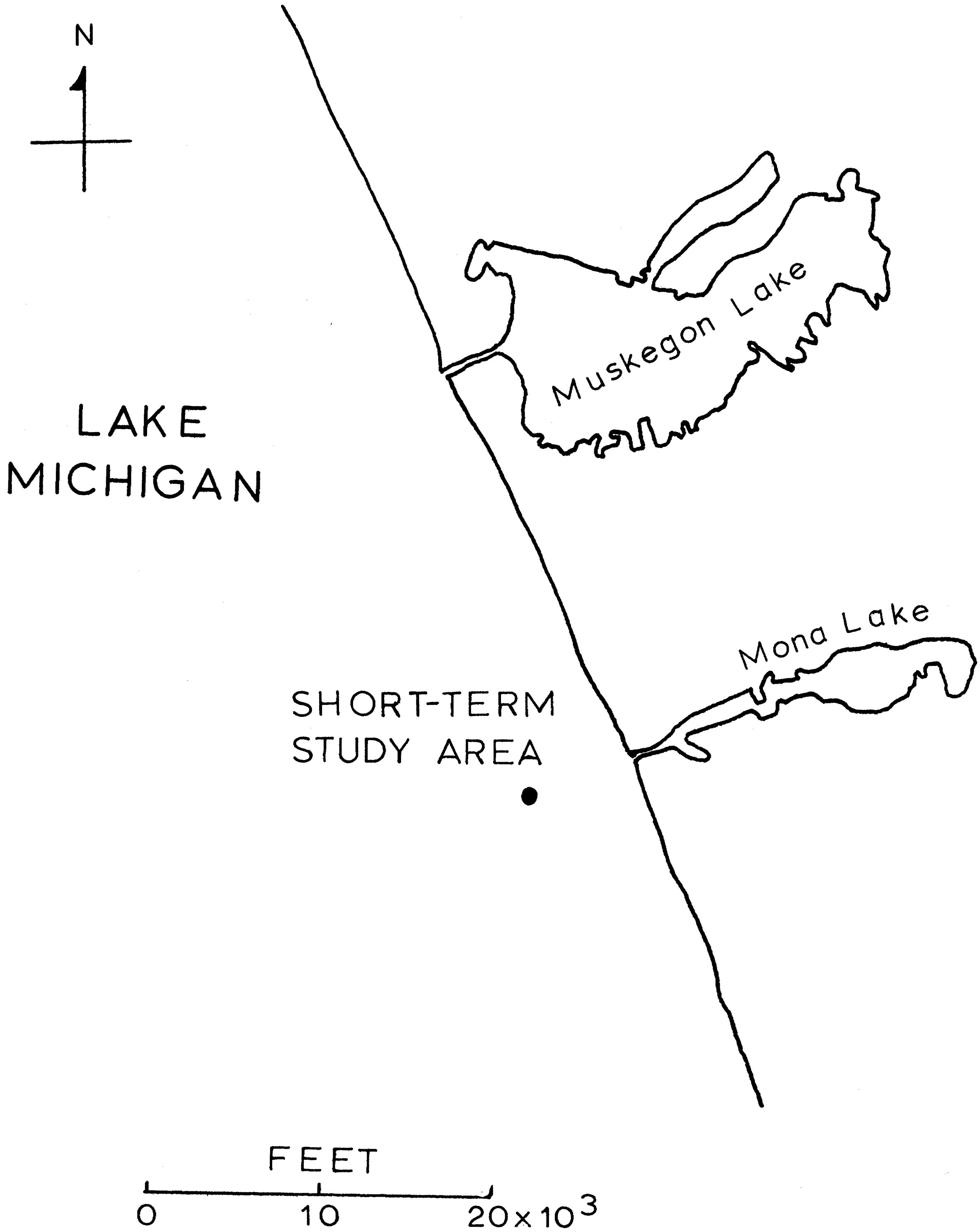

FIG. 2. Location of the short-term study area.

METHODS AND MATERIALS

FIELD SAMPLING PROCEDURES

Long-Term Study Area

The macrobenthos of the long-term study area was sampled in triplicate at each station, on a monthly basis, during three sampling seasons. Data collected during the biological sampling from August 1964 to June 1966 are presented by Ayers and Chandler (1967). Benthic samples were taken with a Smith-McIntyre dredge (McIntyre 1954) (Fig. 3) until June 1965, and with a Ponar grab sampler thereafter (Powers and Robertson 1967) (Figs. 4 and 5).

Powers and Robertson have shown that the Ponar and Smith-McIntyre are comparable in their sampling efficiencies. The Ponar has proved to be a more desirable sampler because the Smith-McIntyre is large and unwieldy, mechanically complicated, and the jaws are subject to premature closing. The powerful tripping springs of the Smith-McIntyre render it dangerous, and at least two men are required to operate it.

Data collection was carried out by two Great Lakes Research Division ships, the R/V MYSIS and the R/V INLAND SEAS. Each vessel was equipped with radar, Raytheon fathometer, hydrographic and heavy duty winches, and the complete complement of limnological, oceanographic, and meteorological equipment necessary for large scale

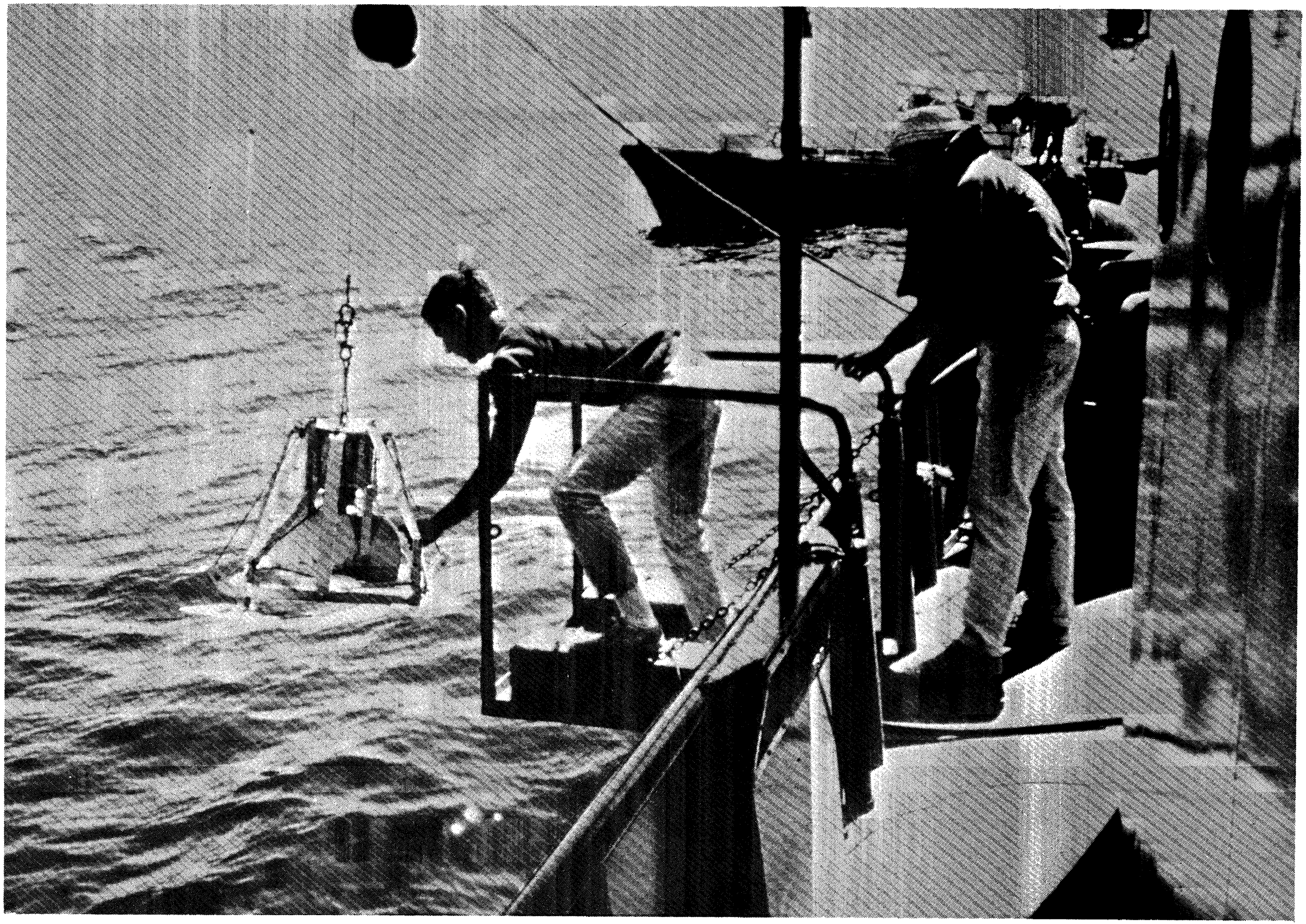

FIG. 3. Smith-McIntyre dredge in opened position, being readied for sampling.

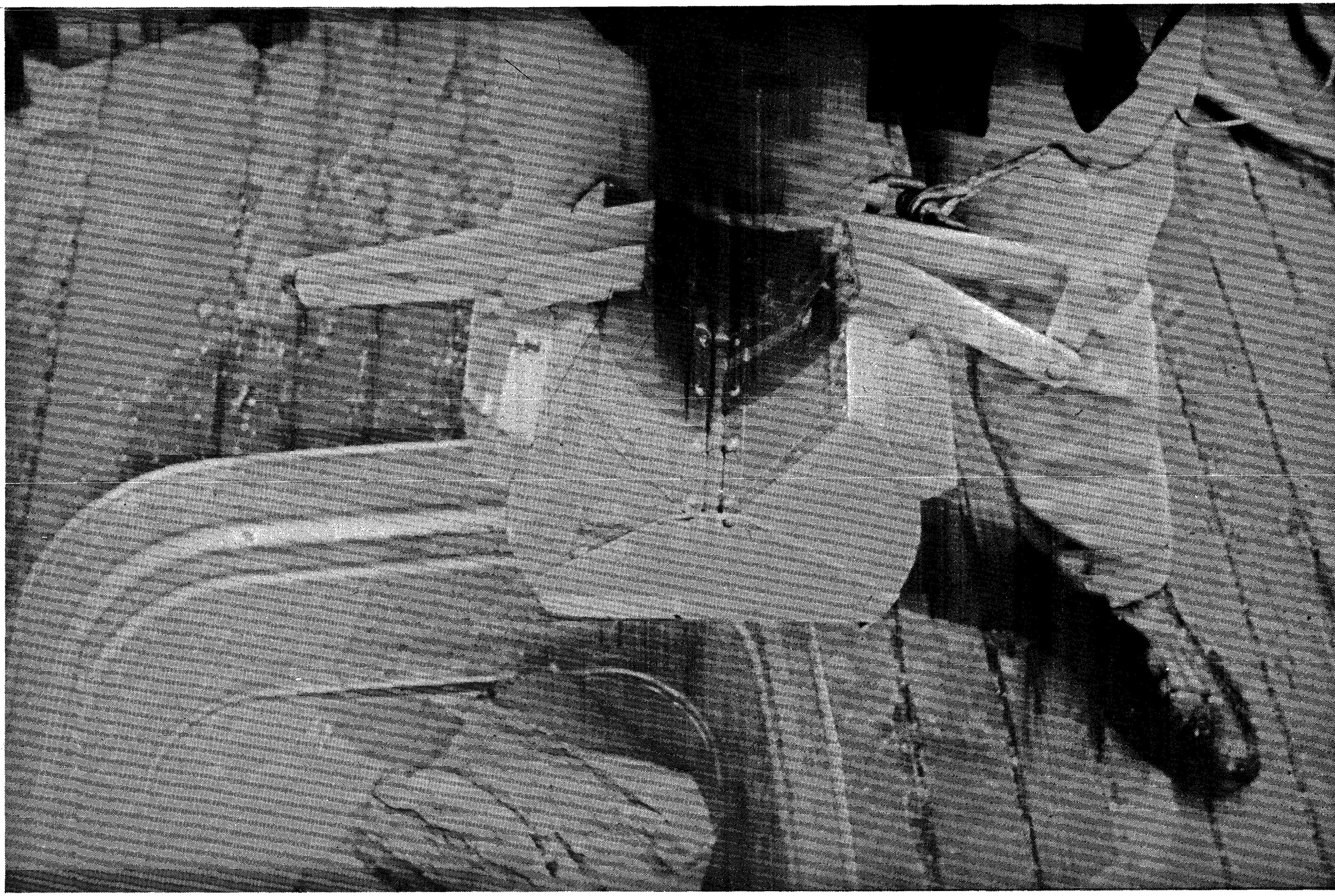

FIG. 4. Ponar grab sampler in open position, showing screened top, side plates, and tripping mechanism.

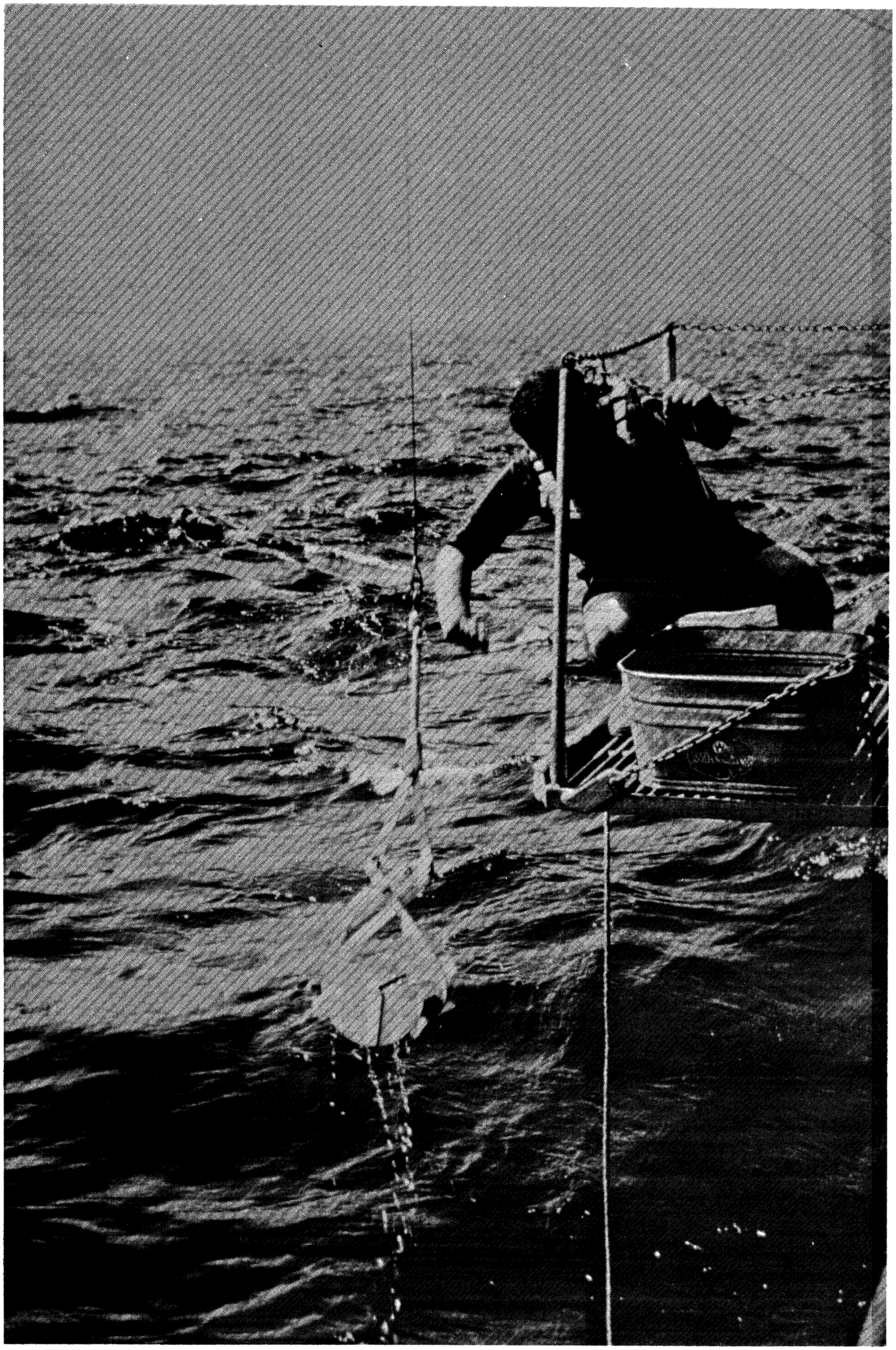

FIG. 5. Ponar grab sampler in closed position, being brought on deck.

investigations. The standard on-station procedure during the macrobenthos sampling was: the ship was stopped on station; the depth, in feet, was recorded from the fathometer and converted to meters; standard marine meteorological observations were taken; water transparency was determined by a white secchi disk; the surface temperature was measured with a thermistor; a bathythermograph cast was made; and three bottom grab samples were taken.

The sampler was opened and the sediment transferred into a large washtub in an undisturbed condition. The sediment texture was classified as sand, sandy silt, silt, layered, and hard bottom after the method described by Powers and Robertson (1968). Layered sediment consisted of a layering of silt-clayey silt over stiff plastic clay, and the hard bottom sediments included gravel, pebbles, and glacial till.

The macrobenthic invertebrates were separated from the sediment by means of an elutriation-screening device (Powers and Robertson 1965) (Fig. 6). A whole sample, including washings from the bottom samplers, was transferred from the washtub to the hopper of the separating device. The sediment was agitated by hosing with water after which the hopper was tipped to pour the supernatant water with suspended organisms into an attached cylindrical screen of 0.5 mm mesh. The fine sediments passed through the screen while the organisms were collected in a pint mason jar that was attached to the screen by a canvas sleeve. The hosing, agitation, and decanting were repeated

FIG. 6. The elutriation-screening device used in separating the macrobenthic organisms from the sediments.

until the macrobenthos was separated from most of the sediments. The organisms were preserved with formalin buffered with calcium carbonate.

Triplicate sediment samples for the determination of the organic carbon content of the surficial sediment were taken at each station in July and October 1965 and in April 1966. These samples were kept frozen until analyzed in the laboratory. The sampling of the sediment has been described by Powers and Robertson (1968). They found no significant differences between July, October, and April samples so the average value of each station was considered a constant during the subsequent statistical analyses.

The bottom temperature, read to the nearest 0.1°C, was determined from the bathythermograph (BT) data. Standard observations of wave height were obtained from snyoptic meteorological information collected by three car ferries that daily traverse Lake Michigan. The CITY OF GREENBAY crosses the lake from Frankfort, Mich., to Kewaunee, Wis., on a course that approximates our E transect, while the CITY OF MIDLAND crosses from Ludington, Mich., to Sheboygan, Wis., on a course near our D transect. The CITY OF MADISON crosses from Muskegon, Mich., to Milwaukee, Wis. Its route is somewhat north of our C transect but close enough to give a fair estimate of conditions.

Short-Term Study Area

The macrobenthic fauna of the short-term study area was collected from two 15 x 15 ft areas of the lake bottom, designated study areas 1 and 2. These areas were sampled in detail by divers utilizing a hand coring device patterned after that described by Fager et al. (1966) (Fig. 7). The steel coring tube was 7 inches in length, had an inside diameter of 2.05 inches, and sampled a surface area of 0.022 ft^2. The butt-end of the corer was fitted with an adaptor made of rubber hose, machined so that a wide mouth pint mason jar could be inserted over it.

The 15 x 15 ft "sampling frame" used by R. F. Anderson[1], constructed of steel pipe and supported by 4 legs 3 ft. long, defined the boundaries of the study area. A grid network consisting of plastic line with attached number tags was arranged on top of the frame to position sample transects and to space the samples. The frame also provided support for the divers, permitting sampling with a minimum disturbance to the bottom sediment and organisms.

The frame was assembled on the beach with flotation tubes attached to each corner. It was then towed to the study area, lowered to the bottom, and positioned by the divers. Two divers working together were able to take samples rapidly. A wide mouth mason jar was attached to the coring tube which was then inserted two inches into the

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[1] A study of fish predation on the macrobenthos of Lake Michigan. Paper presented at the 11th Conference on Great Lakes Research, Milwaukee, Wis., 1968.

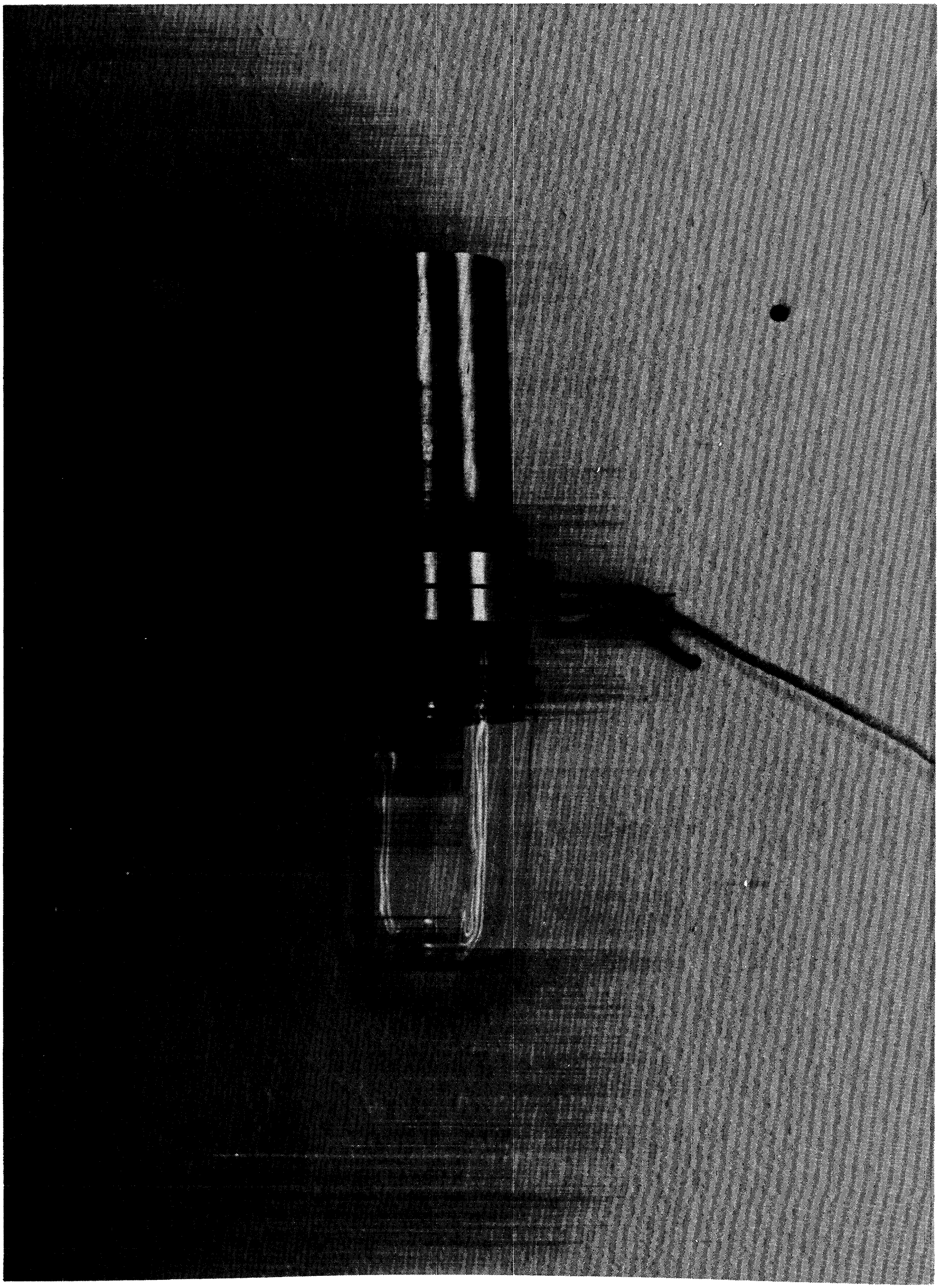


FIG. 7. Hand-coring device used to collect benthos samples at the short-term study area.

bottom. The corer was then tipped to one side, closed off by a metal plate, and inverted, resulting in transfer of the contents to the jar. A numbered lid was placed on the jar after the coring tube had been removed. Divers were able to observe and report any organisms that excaped when the corer was removed from the mason jar. Such losses were rare. Formalin was added as a preservative after the samples were returned to the surface.

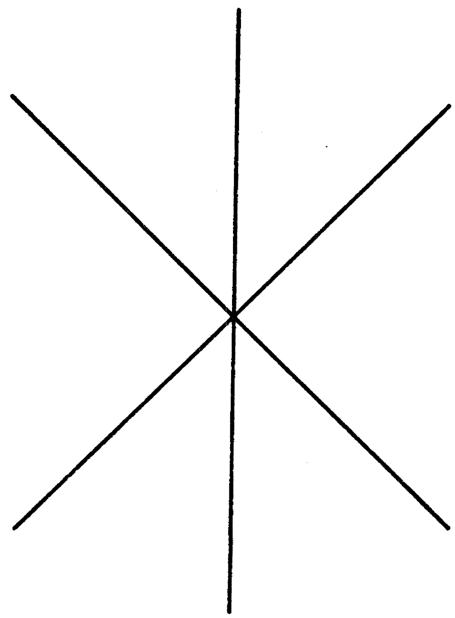
In study area 1 a systematic sampling procedure was utilized. Forty-five samples were taken at 1-ft intervals along 6 transects each 7 1/2 feet long that radiated in a spoke-fashion from the center of the sampling frame (Fig. 8). Two samples were lost. Study area 2 was situated adjacent to study area 1. Forty-five samples, representing triplicates, were taken in 15 randomly chosen quadrats selected from 36 quadrats located within the boundaries of the 15 x 15 ft sampling frame (Fig. 8). The area of each quadrat was 6.25 ft^2.

LABORATORY PROCEDURES

Long-Term Study Area

In the laboratory the organisms and residual sediment of a sample were placed in a white porcelain pan. Each organism was counted and placed in its respective taxonomic group. *Pontoporeia affinis*, Oligochaeta, Sphaeriidae, and Chironomidae constituted the entire sample. Occasionally additional organisms such as leeches, snails,

Study Area 1
Design of the Systematic Sampling Transects



Study Area 2
Design of the Random Sampling Area
(Asterisks Indicate Quadrats Sampled)

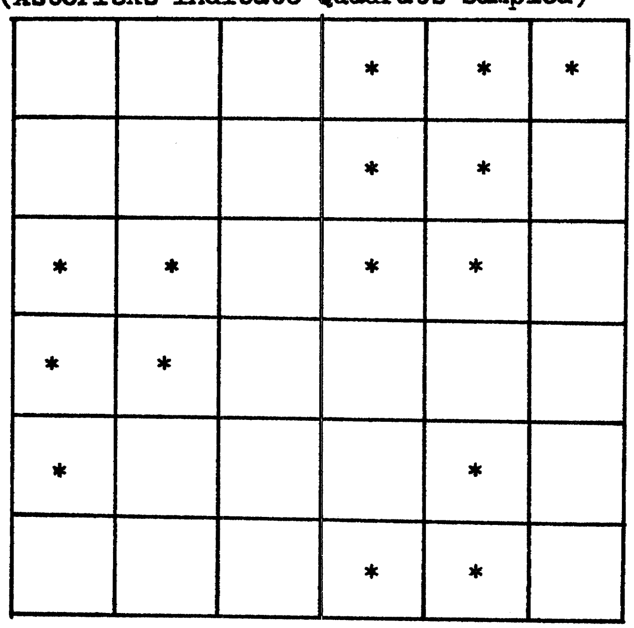


FIG. 8. Design of the systematic and random sampling procedures of the short-term study area.

roundworms, flatworms, mysids, ostracods, and bryozoans were found. They were not included in the analysis because they were not represented through the entire depth regime of the lake.

The telson-rostrum length of Pontoporeia from stations A-5, B-4, B-5, B-6, B-8, E-2, and E-6 for the late April-early May, late May-early June, and October sampling periods of 1965 was measured to the nearest millimeter with an ocular micrometer inserted in a dissecting microscope. The telson-rostrum length was also measured for the first five stations of the C transect for the 1965 and 1966 sampling seasons. At first each specimen was straightened with a pair of dissecting needles during the measurement but it soon became apparent that the organisms were telescopic and that this straightening procedure resulted in some bias. It was found, by comparing straightened organisms with organisms lying in their natural state, that with experience they could be measured accurately while they remained in their natural position.

The brood chamber of each adult female from stations of the A, B, C, and E transects for the 1965 sampling season and the late March-early April, late April, and early June sampling periods of 1966 was examined to determine whether it was brooding or spent. Brooding and spent female amphipods were recorded for the first five stations of the C transect for the entire 1966 sampling season.

Short-Term Study Area

The organisms were separated from the sediment using No. 5

bolting cloth (0.282 mm aperature size), counted and placed in major taxonomic categories. The taxonomic groups considered were the same as for the long-term study: Pontoporeia affinis, Oligochaeta, Chironomidae, and Sphaeriidae. The individuals within the Pontoporeia population were of two size groups, approximately 2 mm and 7 mm in length, and each group was treated independently during subsequent analysis.

RESULTS

LIFE HISTORY AND REPRODUCTION

The development of *Pontoporeia affinis* is direct through the immature instars. Sexes become distinguishable in later instars on the basis of oöstegite formation in the females and increased length of the antennal flagella of the male (Fig. 9).

The characteristics of the adult male are morphological modifications that are considered adaptions for a pelagic existence. The elongation of the pleopods and the setation of the last uropods increase its swimming capabilities. Segerstråle (1950) felt that the adult male seldom lives longer than one week, and apparently does not feed as its alimentary canal is invariably empty and its mandibles are reduced in size. The adult male ranges from 7 to 9 mm in length in Lake Michigan.

The thoracic region of the adult female becomes more robust in appearance with the development of the large marsupial plates, or oöstegites, that form on the inner surface of the coxal plates of the second to fifth pereiopods. The adult female ranges from 6 to 9 mm in length in Lake Michigan. Juday and Birge (1927) found the number of eggs carried by each adult female ranged from 13-28 with a general average of 20.

The female dies after producing its brood. The body begins to degenerate during the course of the incubatory period, becoming trans-

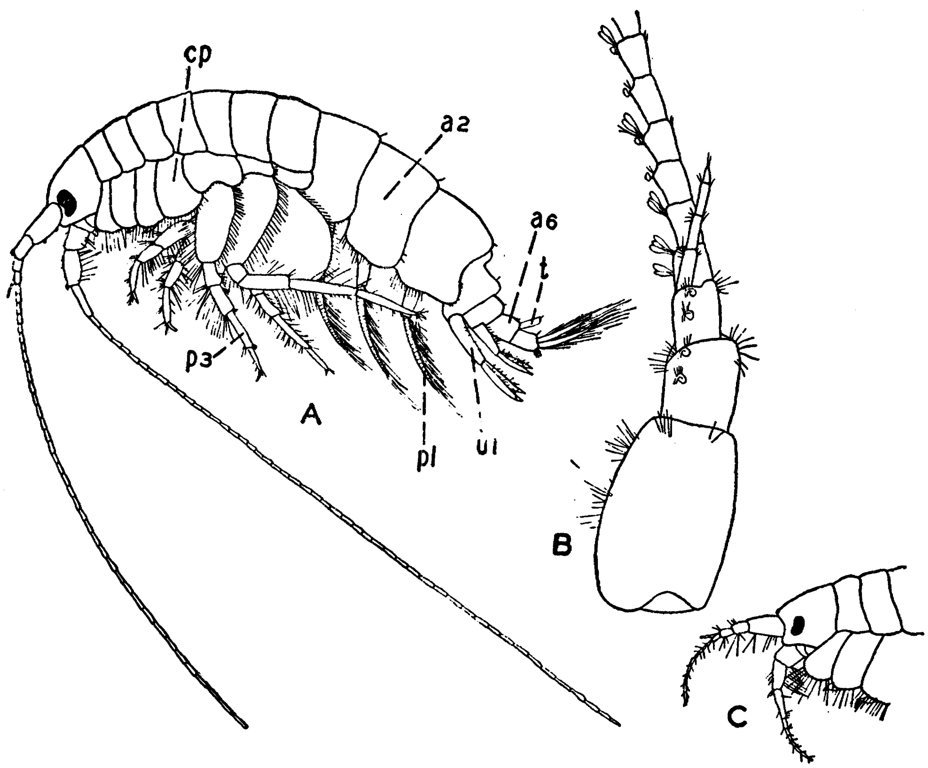


FIG. 9. Morphological features of Pontoporeia affinis. A, male x9; B, basal portion of first antenna of male; C, anterior end of female; a2, second abdominal segment; a6, sixth abdominal segment; cp, coxal plate; p3, third pereiopod; pl, third pleopod; t, telson; ul, first uropod. (Modified from Segerstråle; copied from Pennak)

lucent, while the gills lose their leaf-like form and become thick and opaque. The young are slightly less than 2 mm long when they are released from the brood pouch. This reporductive cycle distinctly contrasts with most amphipod species which produce successive broods at intervals of a few weeks during the summer months.

During the daylight hours, in the shallower inshore regions, the Pontoporeia population remains burrowed in the surficial sediments, but at night some members of the population make excursions up into the water column. However, C. F. Powers (personnal communication), in observations made while participating in the 1967 STAR II submersible dives in Lake Michigan, reported seeing large numbers of adult males swimming in the water column in the deeper portions of the lake during the daylight hours.

Wells (1960) and Marzolf (1965) reported nocturnal vertical migrations of Pontoporeia in Lake Michigan. Marzolf sampled the bottom sediments while examining the vertical migrations and found that only the larger amphipods migrated while the majority remained in the surficial sediments. Segerstråle (1950) noted that adult males spend a longer time above the bottom than adult females and immature organisms. Mating is thought to occur during the nocturnal migrations of the adult males and females.

Brooding and spent females were found in the lake as early as the 21 March and occurred in certain localities until November (Tables 2 and 3).

TABLE 2. Monthly occurrence of brooding (B) and spent (S) female *Pontoporeia affinis* in Lake Michigan for 1965. O represents no brooding or spent females; - represents no data.

Station	Depth (Meters)	17 Apr. -4 May	16 May -4 June	22 June -2 July	13-20 July	9-14 Aug.	7-20 Sept.	1-15 Oct.	4-9 Nov.
A-1	18	S	0	0	0	0	0	0	0
A-2	35	S	0	0	B	0	0	0	0
A-3	70	0	B	B	S	B	-	0	0
A-4	74	0	0	0	B	B	S	0	0
A-5	43	B	B	B	-	0	-	0	0
A-6	18	B	0	0	0	0	0	-	-
B-1	19	B	0	0	0	0	0	0	0
B-2	47	B	B	B	B	B&S	0	S	0
B-3	68	-	-	0	B	B&S	-	B	B&S
B-4	129	-	0	0	B	B&S	S	0	0
B-5	108	S	S	S	B	B	0	S	0
B-6	83	0	0	-	B	0	B	0	0
B-7	45	B	B	B	-	0	0	0	0
B-8	11	S	0	0	0	0	0	0	0
C-1	20	B	0	0	-	0	0	0	0
C-2	50	B	B	0	-	B&S	S	0	0
C-3	77	B	S	0	-	B&S	B&S	0	B&S
C-4	108	-	S	0	-	0	0	0	B
C-5	157	B	0	0	-	0	0	0	0
C-6	99	-	0	0	-	B	0	0	0
C-7	55	B	B	0	-	B	0	0	0
E-1	44	S	0	-	-	0	0	0	B
E-2	197	B	0	-	-	0	0	S	B
E-3	271	-	0	-	-	0	0	0	B
E-4	216	0	0	-	-	0	0	0	-
E-5	173	0	0	-	-	B	S	0	B&S
E-6	33	B	0	-	-	0	0	0	0

TABLE 3. Monthly occurrence of brooding (B) and spent (S) female Pontoporeia affinis in Lake Michigan for 1966. 0 represents no observed brooding or spent females; - represents no data.

Station	Depth (Meters)	21 Mar. -7 Apr.	25-30 Apr.	1-6 June	27 June	10 Aug.	29 Aug.	26 Sept.	9 Nov.
A-1	18	B	S	0	-	-	-	-	-
A-2	35	-	B&S	0	-	-	-	-	-
A-3	70	-	0	B&S	-	-	-	-	-
A-4	74	-	0	0	-	-	-	-	-
A-5	43	-	B&S	0	-	-	-	-	-
A-6	18	-	B&S	0	-	-	-	-	-
B-1	19	B&S	S	0	-	-	-	-	-
B-2	49	B&S	B&S	B&S	-	-	-	-	-
B-3	68	B&S	B&S	B	-	-	-	-	-
B-4	129	B	0	0	-	-	-	-	-
B-5	108	-	0	B	-	-	-	-	-
B-6	83	0	0	B	-	-	-	-	-
B-7	45	-	B&S	B&S	-	-	-	-	-
B-8	11	B&S	0	0	-	-	-	-	-
C-1	20	B&S	B&S	0	0	0	0	0	0
C-2	50	B&S	B&S	B	B	0	B	0	0
C-3	77	B&S	0	B	B	0	S	S	0
C-4	108	0	0	0	B	0	0	0	B
C-5	157	-	B	0	S	0	0	0	0
C-6	99	0	-	0	0	-	-	-	-
C-7	55	B&S	-	B	B	-	-	-	-
E-1	44	B&S	-	0	-	-	-	-	-
E-2	197	-	-	B	-	-	-	-	-
E-3	271	-	-	0	-	-	-	-	-
E-4	216	0	-	B	-	-	-	-	-
E-5	173	-	-	0	-	-	-	-	-
E-6	33	S	-	0	-	-	-	-	-

The only winter benthic samples were obtained at stations C-1, C-2, and C-3 on 27 January 1967, and no brooding or spent females were observed in those samples.

It appeared that at depths less than 35 m, in Lake Michigan, reproduction is completed by late May-early June. Beyond 35 m it seemed that Pontoporeia bred intermittently throughout the sampling season. An examination of the bottom temperature records indicated that this amphipod did not breed at any depth when the bottom temperature exceeded 7°C.

The fact that adults die after reproduction simplifies the recognition of year classes. The size frequency distributions for station B-8, average depth 11 m, described a population of amphipods that matured in one year (Fig. 10). The two major size groups of 2 May indicated that the population was in the middle of the breeding season. The large 2 mm size group and small proportion of larger individuals on 2 June showed that reproduction was in its terminal phase. The large 5-6 mm size group of 15 October indicated that the cohort of the young of the year has grown approximately 4 mm in six months.

At station E-6 where the average depth was 33 m, amphipods required two years to mature. Both brooding females and newly released young as well as juveniles from the previous year were present in the 21 April sample. Recently released young, juveniles from the previous year, and a few adults were present in the 2 June sample. The two size groups of the 5 October sample represented the young of the year and the

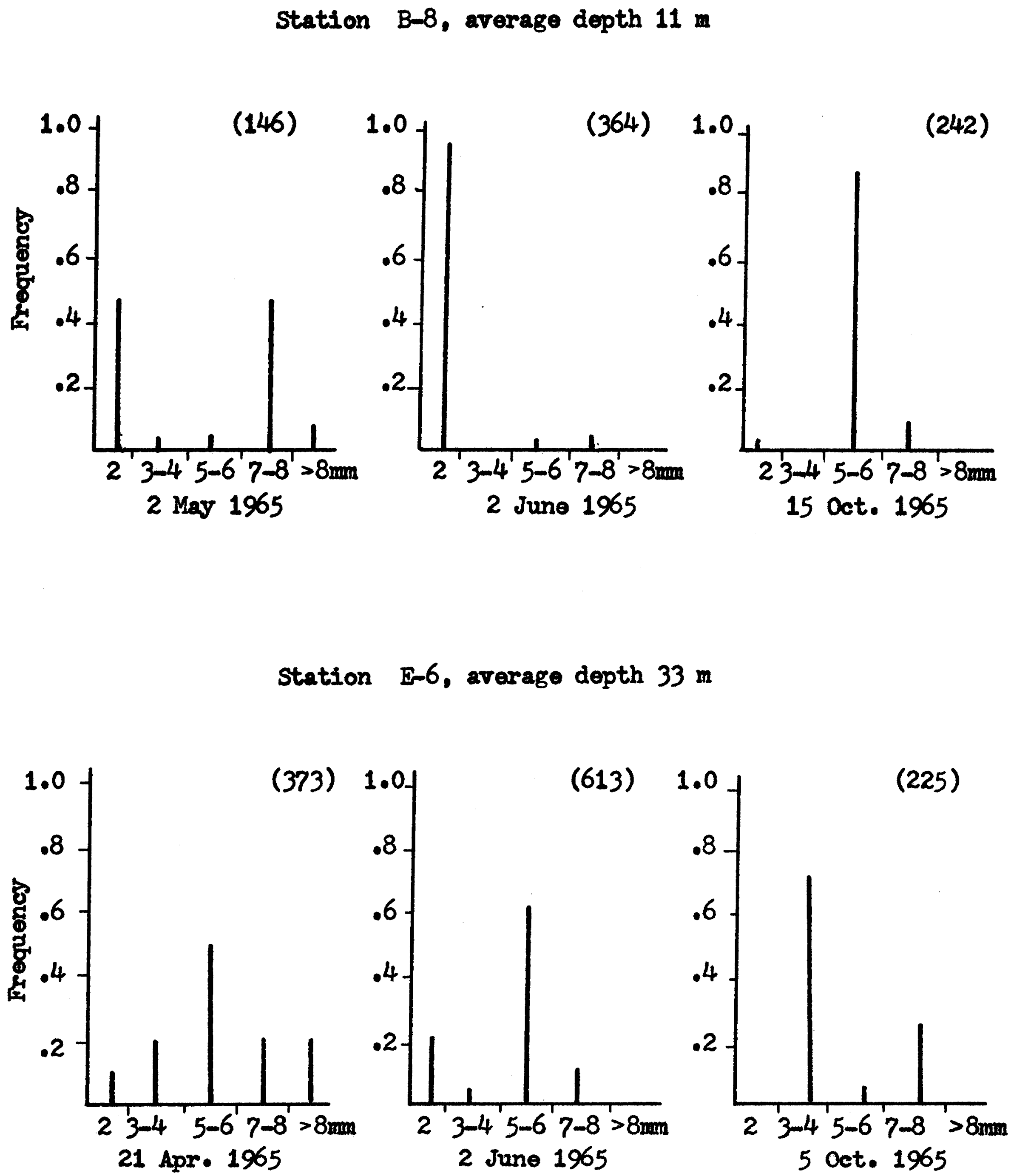


FIG. 10. Size frequency histograms of Pontoporeia affinis for selected depths of three sampling periods late April-early May, late May-early June, and early October 1965. Number in parenthesis represents the sample size.

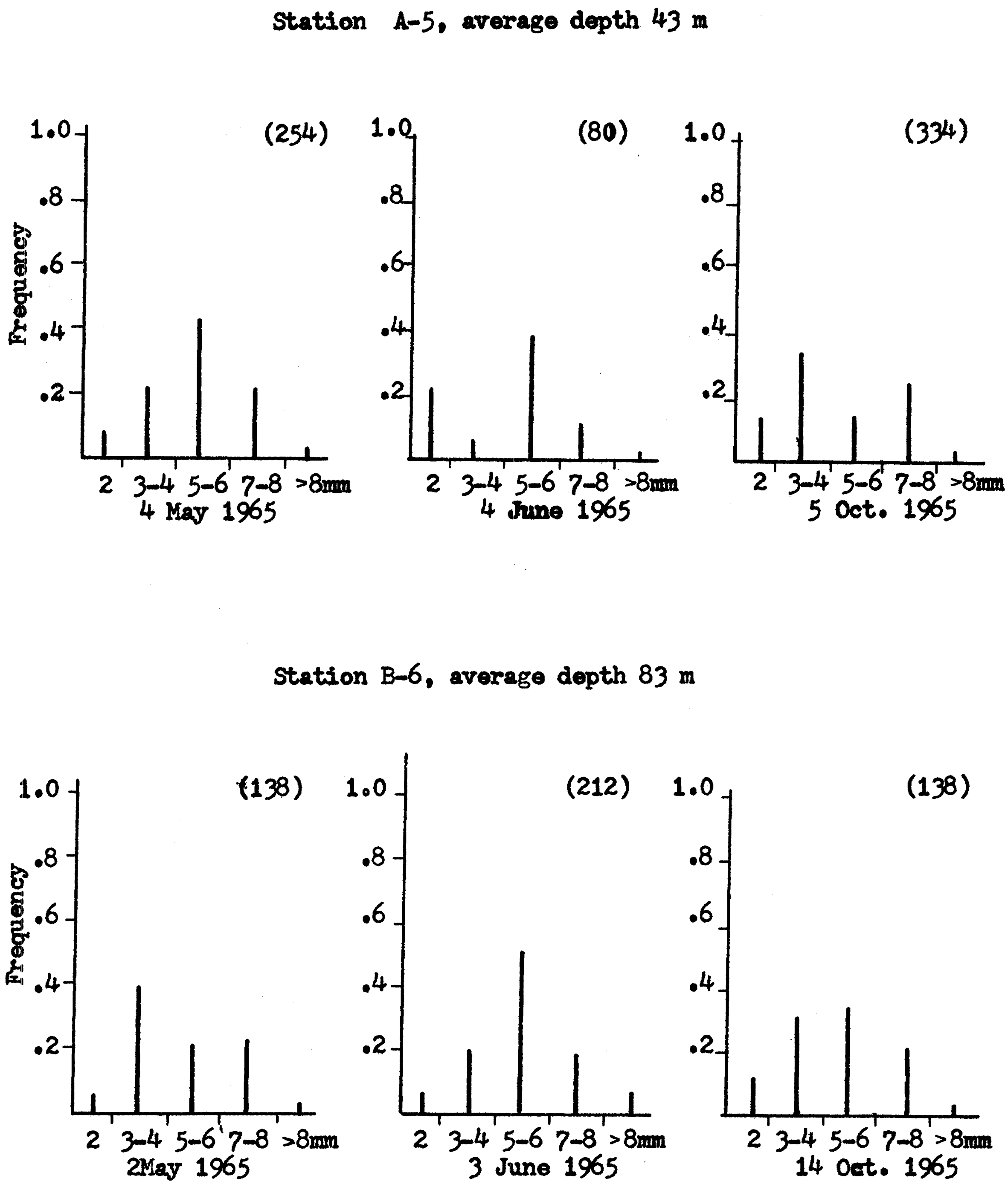
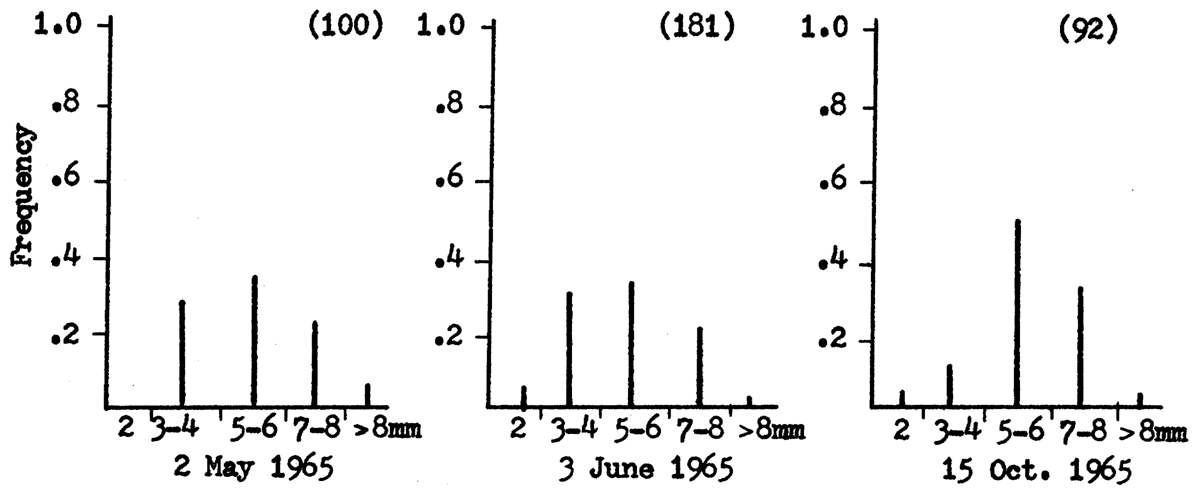


FIG. 10. Continued.

Station B-5, average depth 108 m



Station B-4, average depth 129 m

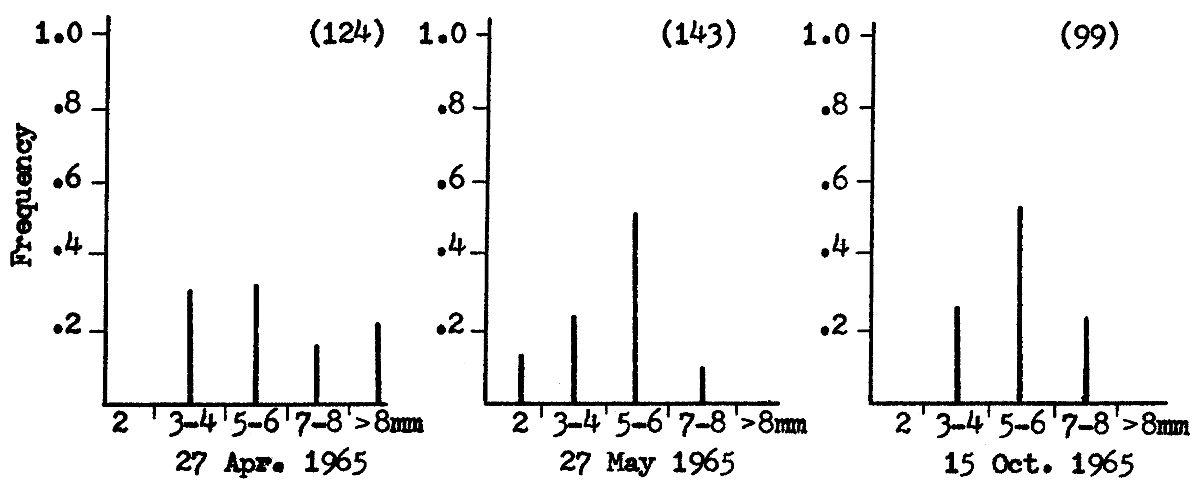


FIG. 10. Continued.

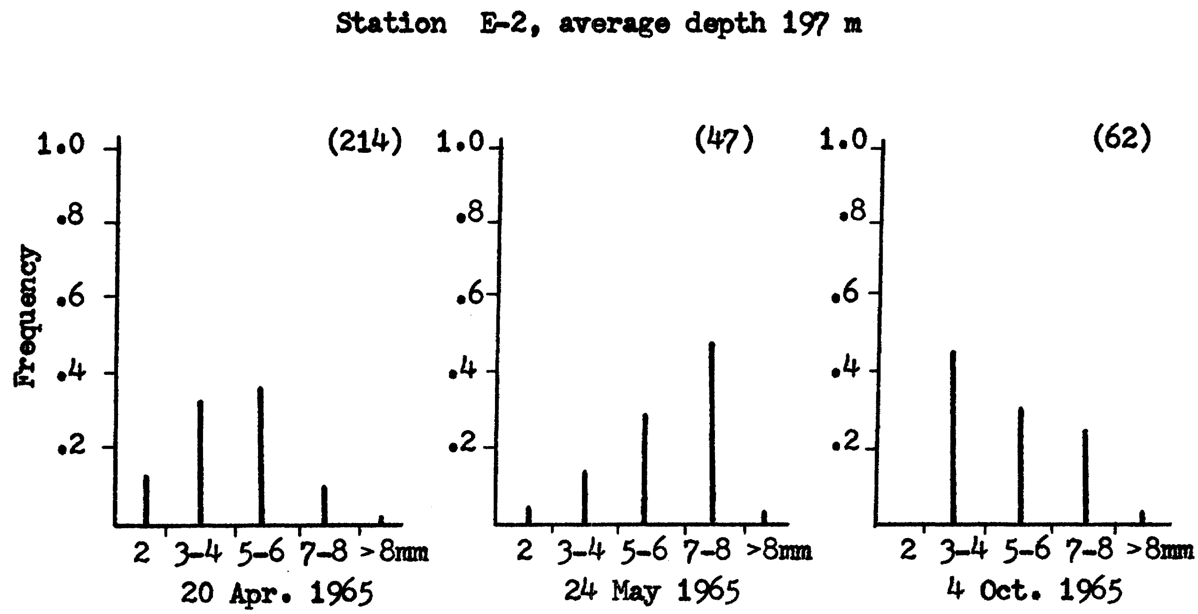


FIG. 10. Continued.

young of the previous year. At this station, growth was less than 2 mm for the 6 month interval from April to October, which was about half that observed at B-8.

Figure 10 also shows that stations deeper than 35 m have size frequency histograms for Pontoporeia which are similar to each other. In the 35-86 m depth zone a larger proportion of individuals fell in the 2 mm size interval than was the case in deeper regions of the lake. It was difficult to determine how much time is required for the maturation of Pontoporeia at depths greater than 35 m.

Monthly size frequency histograms were made for stations C-1, C-2, C-3, C-4, and C-5 for April to November 1965 and from March to November 1966 (Figs. 11 to 15). Pontoporeia found at station C-1, average depth 20 m, also required two years to mature. The remaining four C stations were positioned in waters deeper than 35 m. Stations C-2 and C-3 lay in the 35 to 86 m depth zone and showed a higher proportion of individuals in the 2 mm size class than did stations C-4 and C-5 which were in deeper waters.

PATTERNS OF SPATIAL DISTRIBUTION

Short-Term Study Area

Patterns of spatial distribution in the short-term study area were examined by two methods: by plotting the mean against the variance and by examining the occurrence frequency of the number of individuals per quadrat. If the mean number of individuals per quadrat is independent

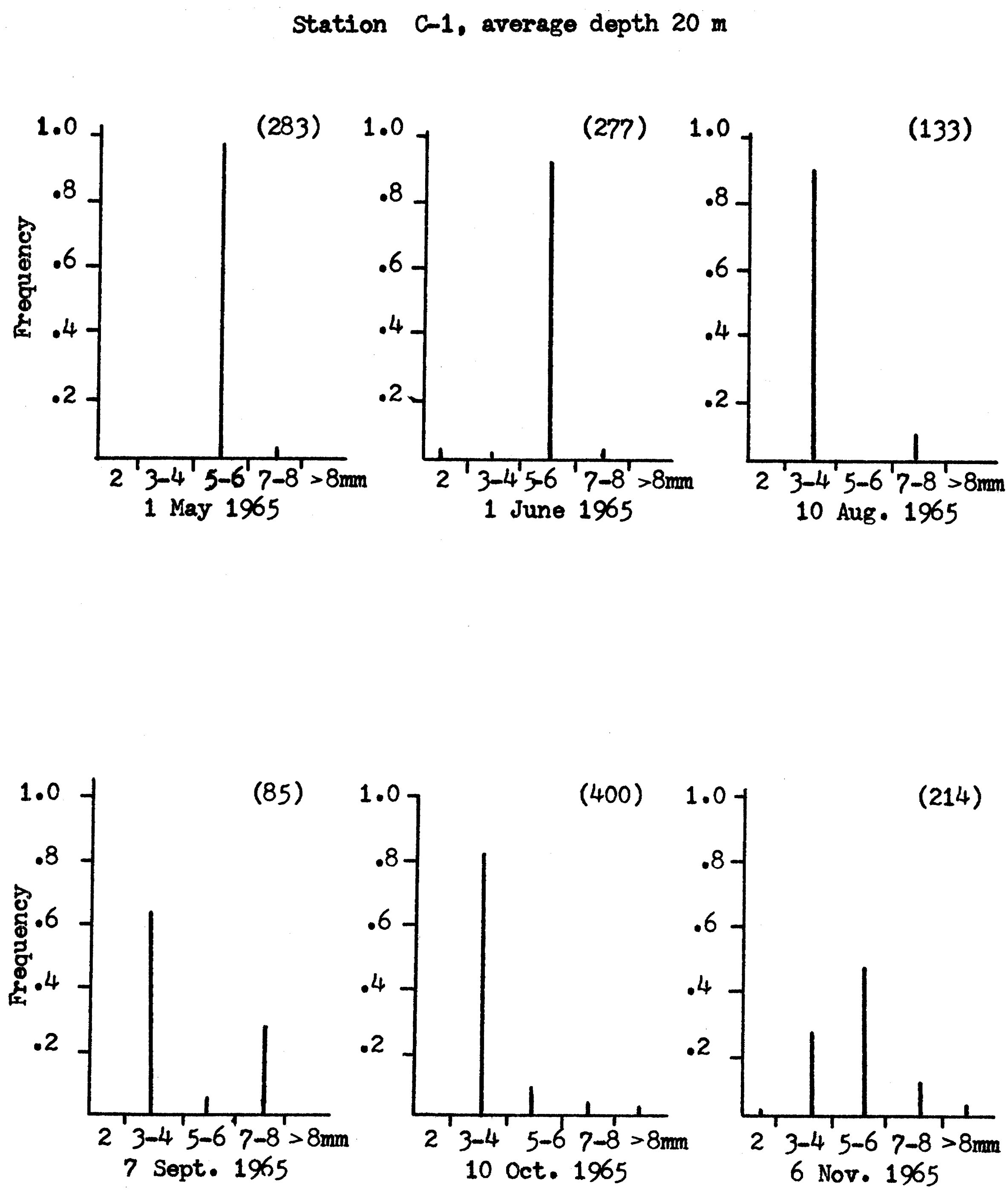


FIG. 11. Size frequency histograms of Pontoporeia affinis collected at station C-1 for the 1965 and 1966 sampling seasons. Number in parenthesis represents sample size.

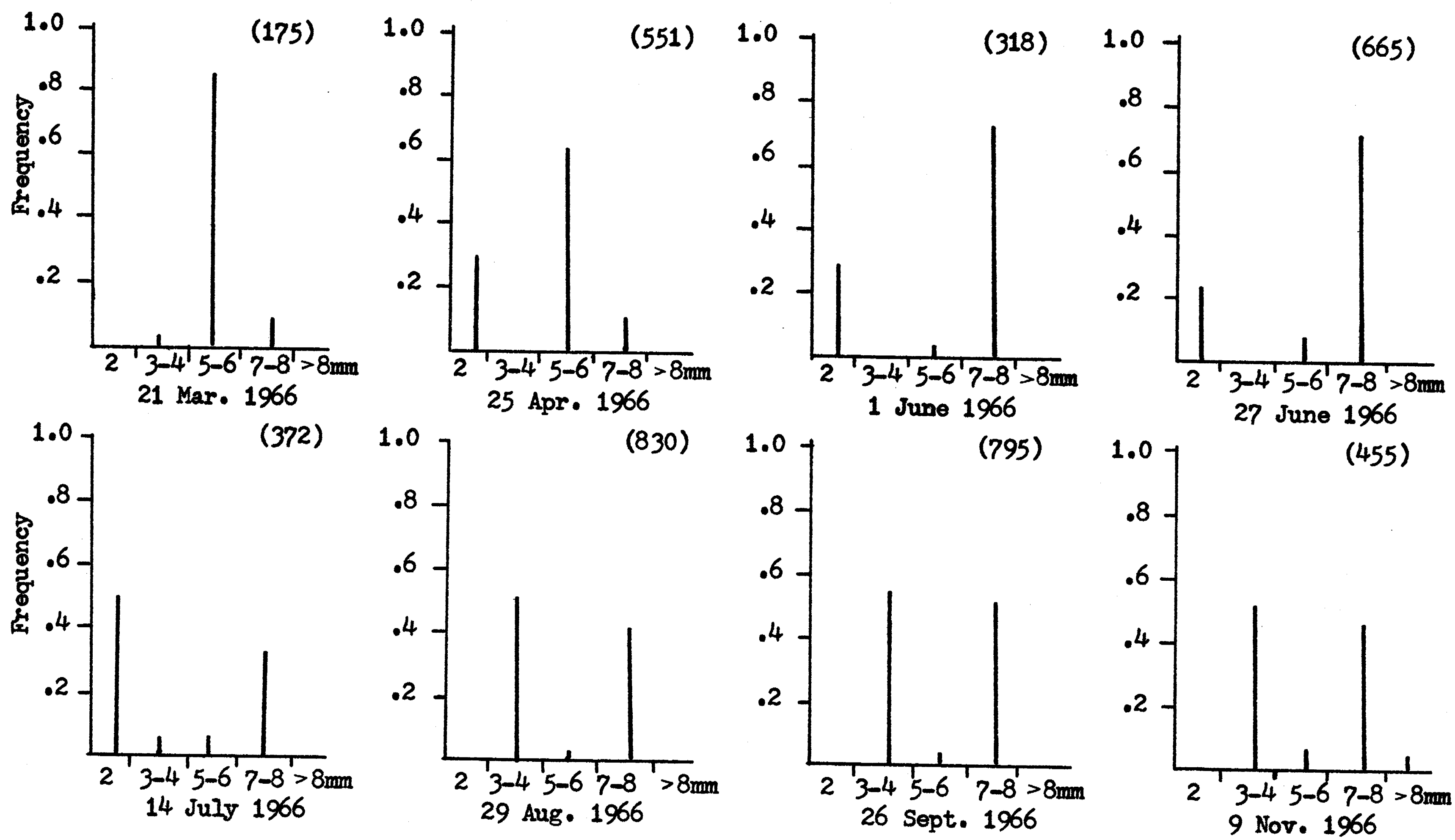


FIG. 11. Continued.

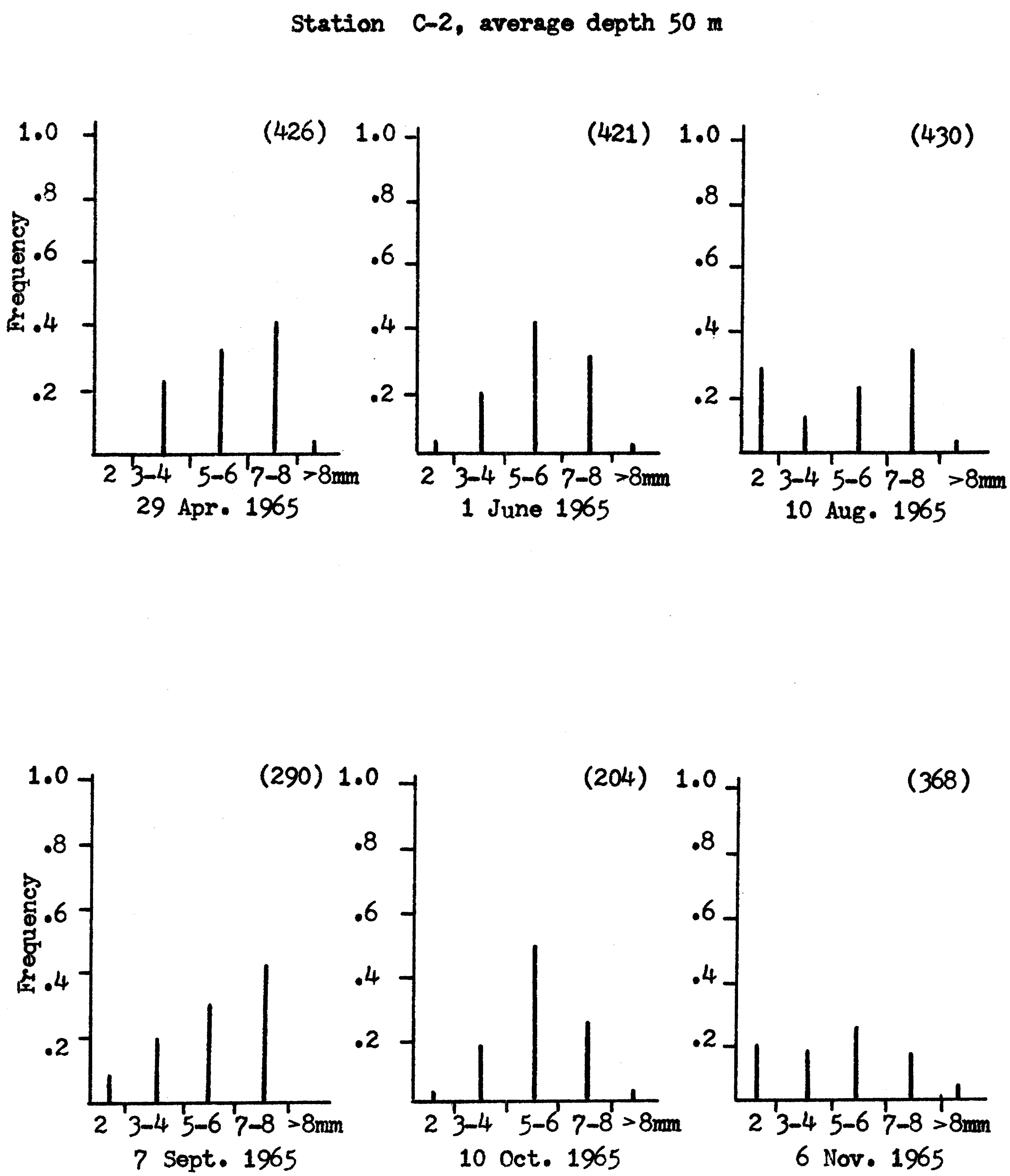


FIG. 12. Size frequency histograms of Pontoporeia affinis collected at station C-2 for the 1965 and 1966 sampling seasons. Number in parenthesis represents the sample size.

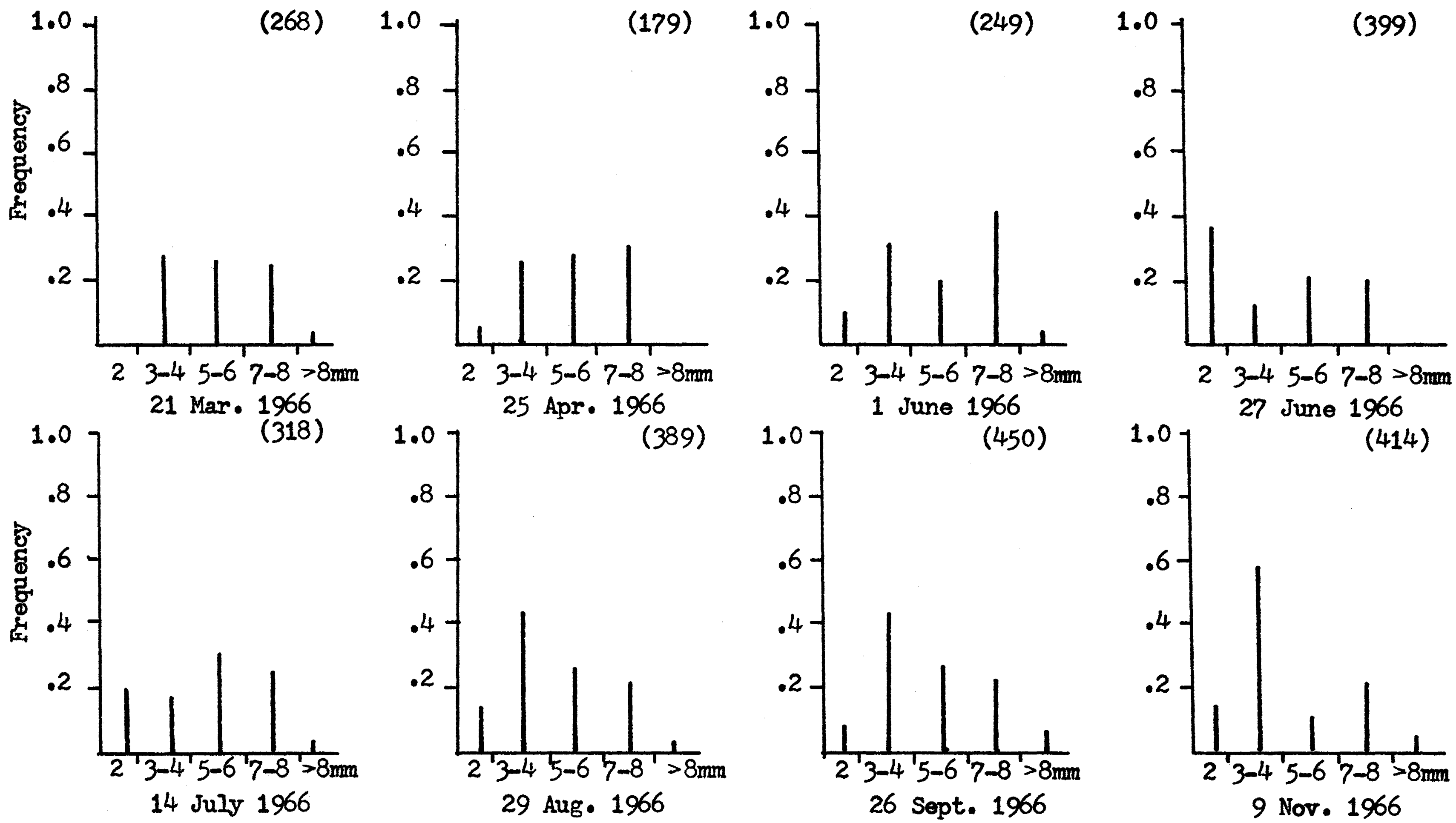


FIG. 12. Continued.

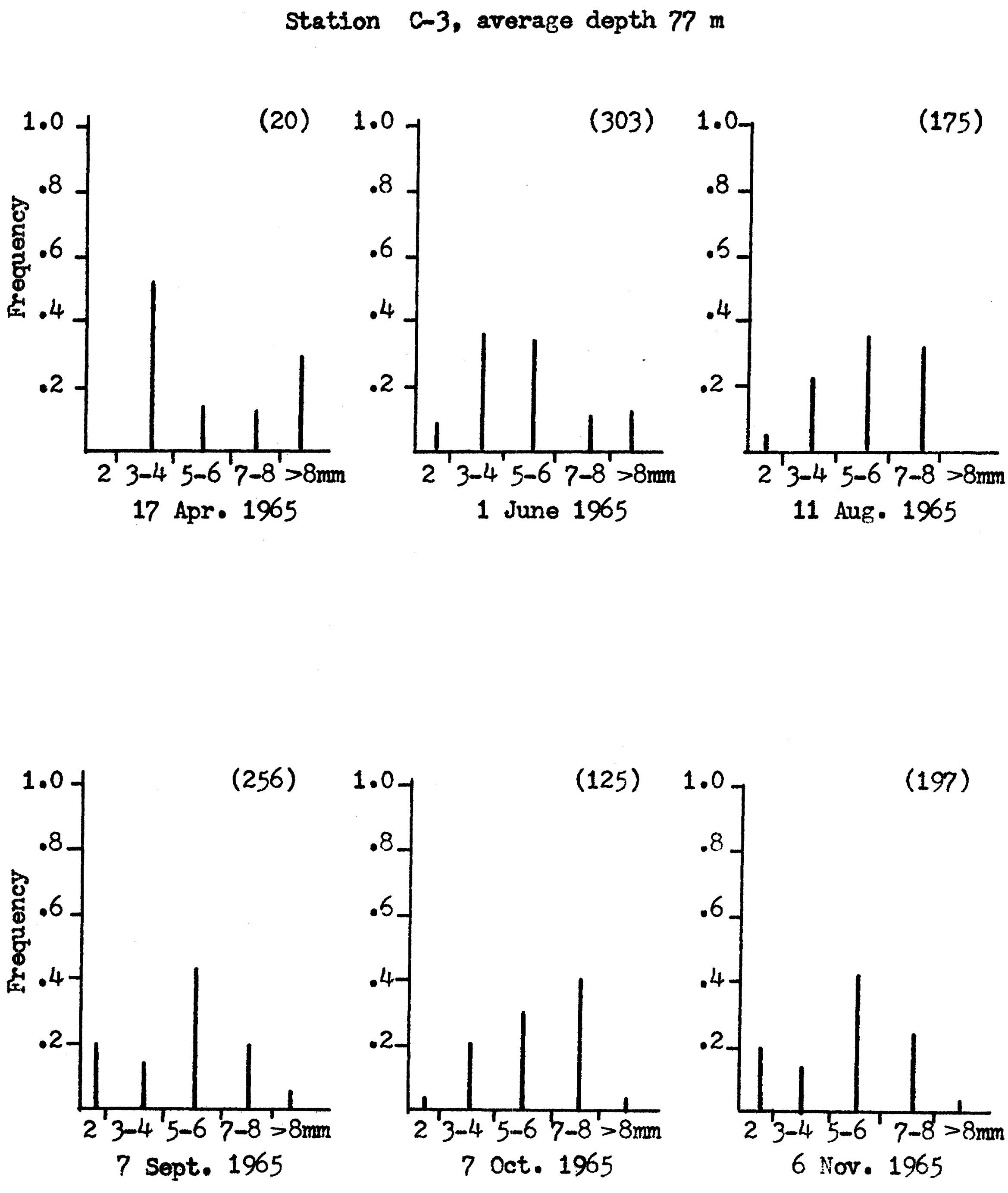


FIG. 13. Size frequency histogram of Pontoporeia affinis collected at station C-3 for the 1965 and 1966 sampling seasons. Number in parenthesis represents sample size.

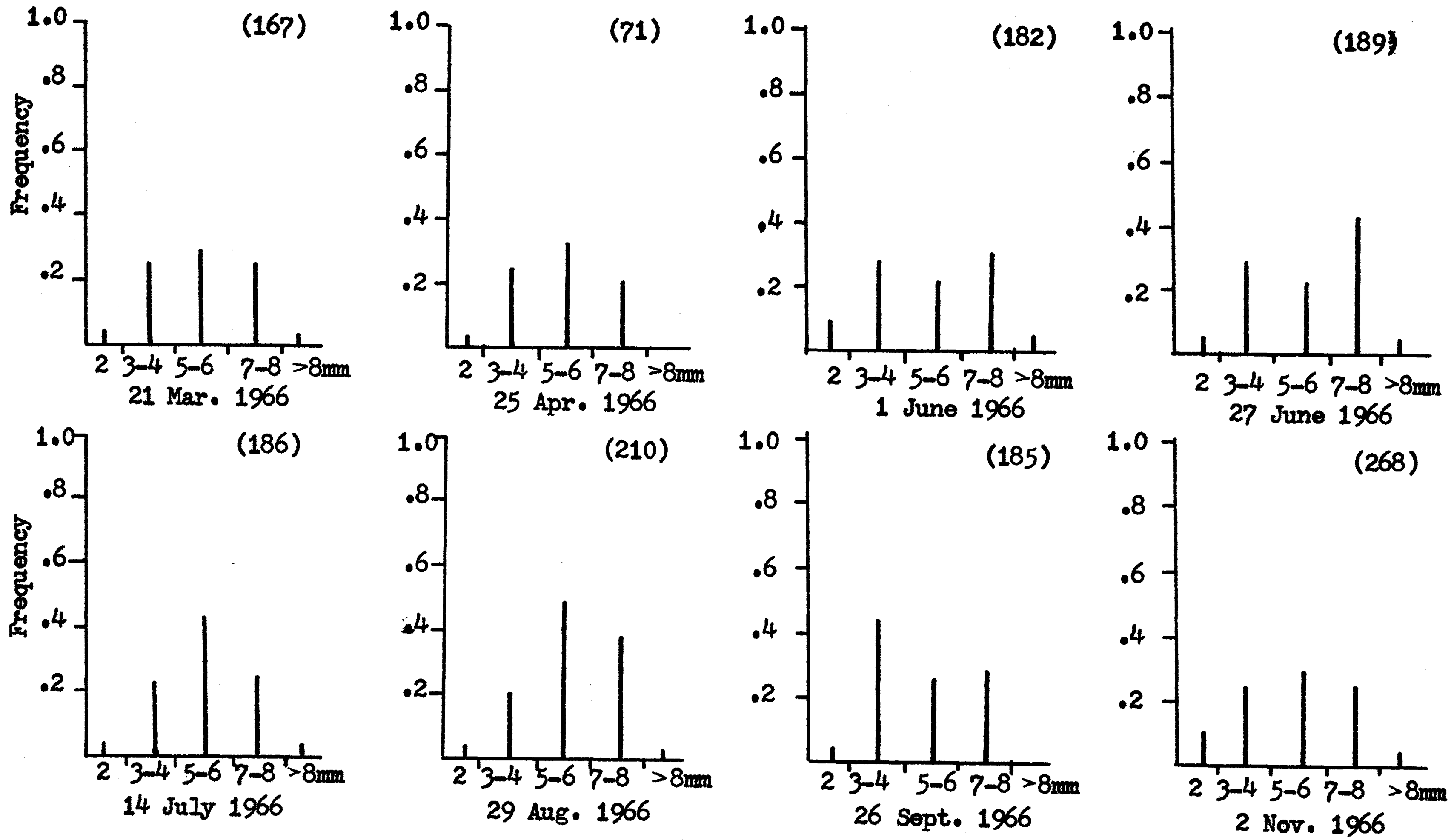


FIG. 13. Continued.

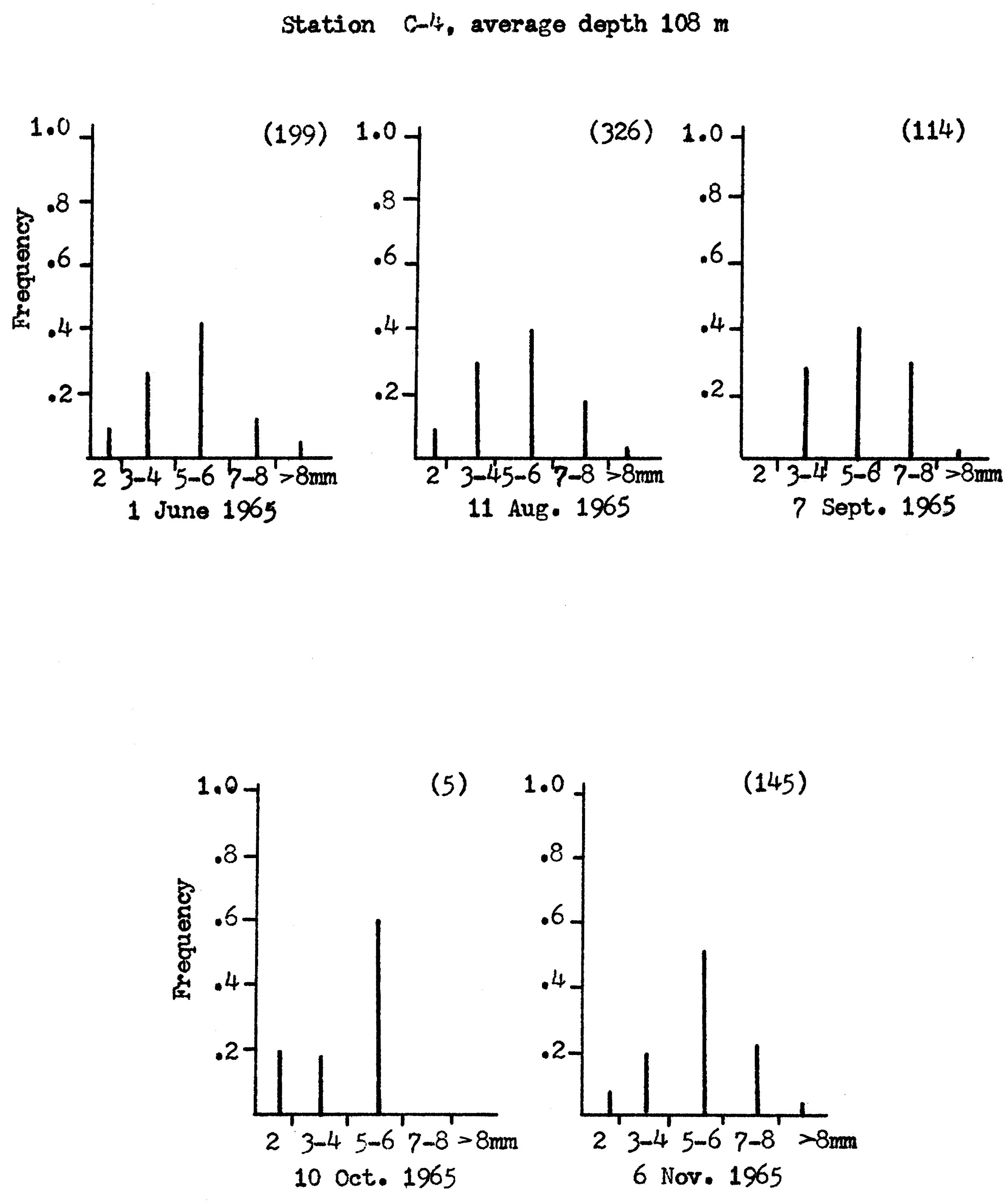


FIG. 14. Size frequency histograms of Pontoporeia affinis collected at station C-4 for the 1965 and 1966 sampling seasons. Number in parenthesis represents the sample size.

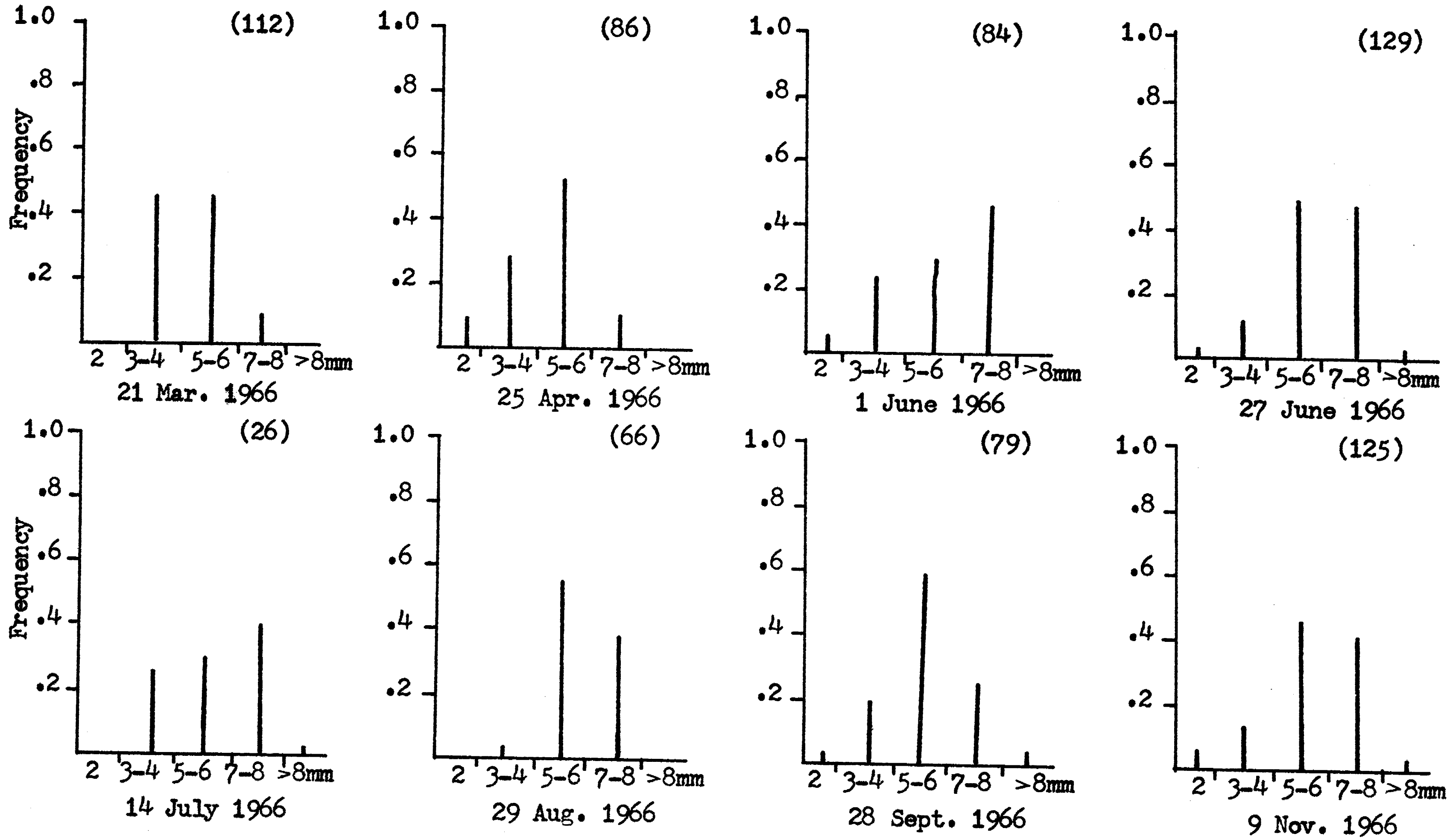


FIG. 14. Continued.

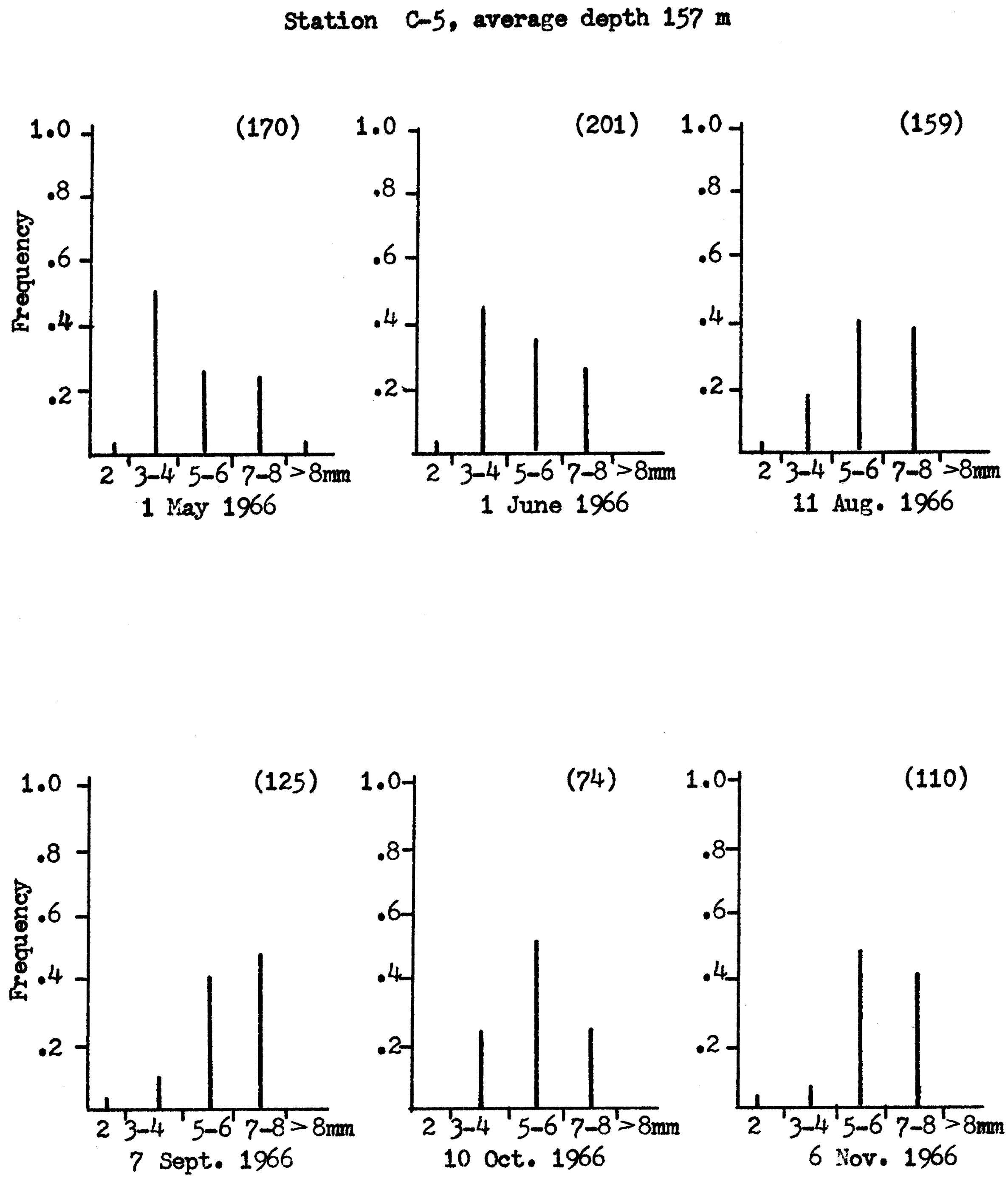


FIG. 15. Size frequency histograms of Pontoporeia affinis collected at station C-5 for the 1965 and 1966 sampling seasons. Number in parenthesis represents sample size.

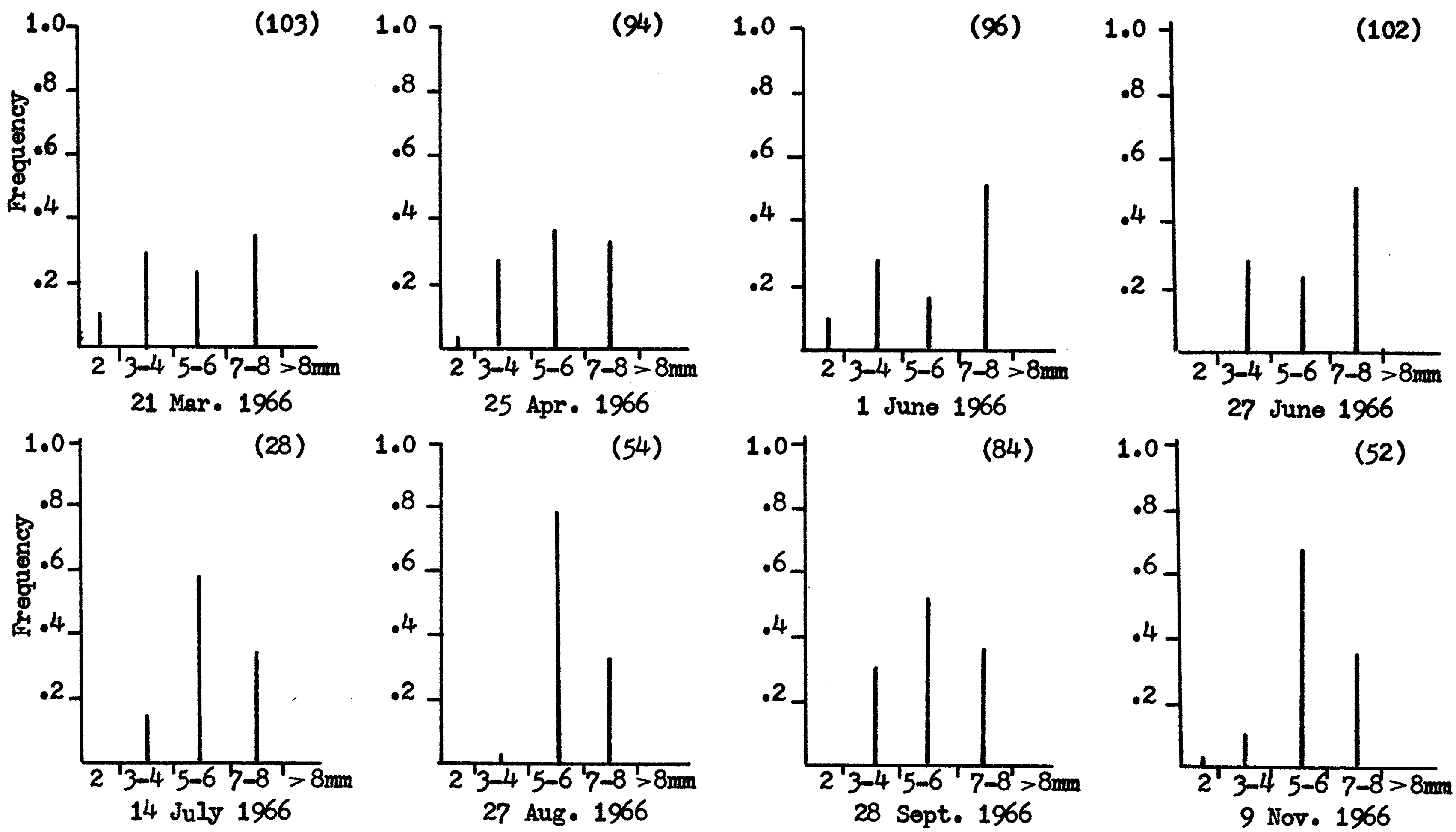


FIG. 15. Continued.

of its variance, then the population is normally distributed. If the mean is proportional to the variance and the mean-variance regression has an intercept of zero and a regression coefficient of 1, then the population conforms to the Poisson distribution, which implies that the population is randomly distributed within the sampling area.

The mean and variance of the 15 sets of triplicate samples from the short-term study area 2 were plotted against each other for the small, large, and total Pontoporeia (Figs. 16-18). The resulting correlation coefficients indicate that the mean is independent of the variance for small and total Pontoporeia ($r = .226$ and $.415$, d. f. = 13) and that these two groups conform to the normal distribution. On the other hand, both the mean-variance regression coefficient and the intercept are approximately one for large Pontoporeia, suggesting a Poisson distribution.

The occurrence frequency for the numbers of individuals per quadrat was determined for each of the three categories from the combined 88 samples of study areas 1 and 2. Small and total Pontoporeia were treated in such a fashion that 3 to 7 individuals per interval were combined and called 5, 8 to 12 were combined and designated 10, and so forth.

An examination of the occurrence frequency histograms (Figs. 19-21) indicated that the distribution of small and total Pontoporeia tended toward the normal while large Pontoporeia followed the Poisson distri-

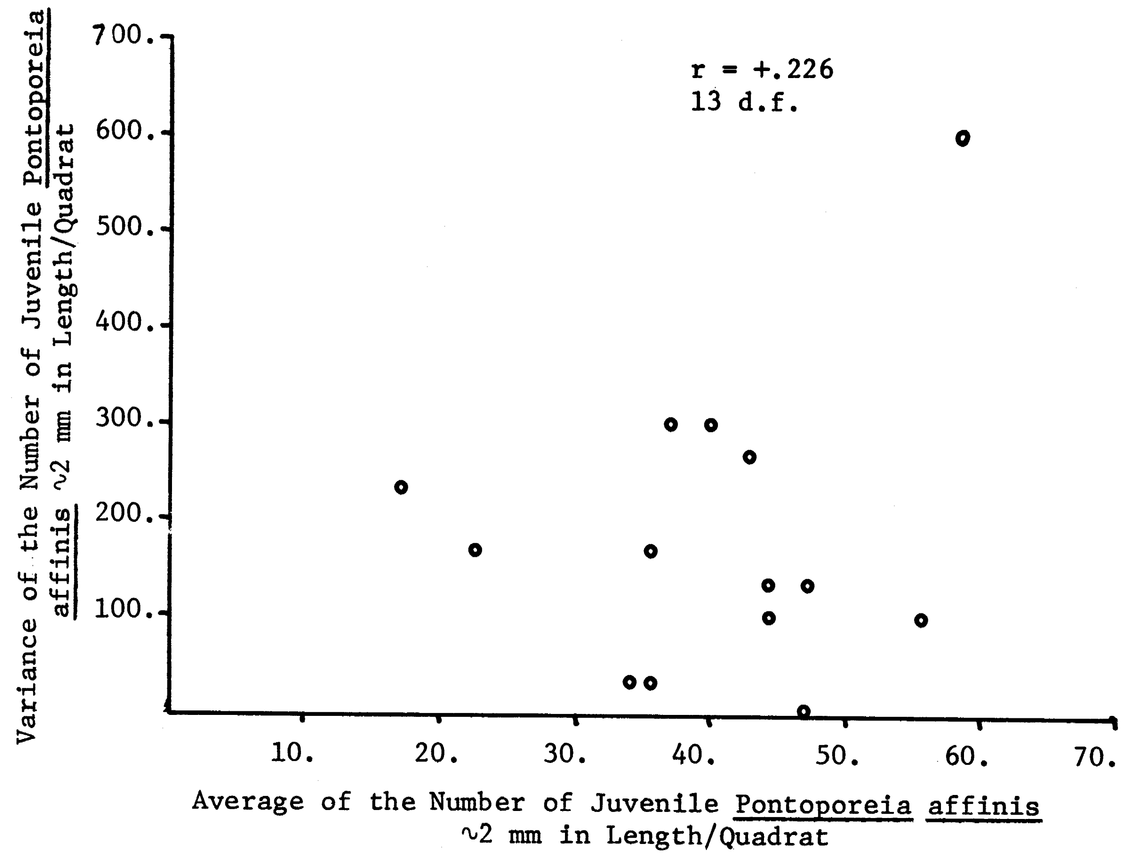


FIG. 16. The variance-mean relationship of juvenile _Pontoporeia affinis_, ~2 mm in length per quadrat, from the short-term study area.

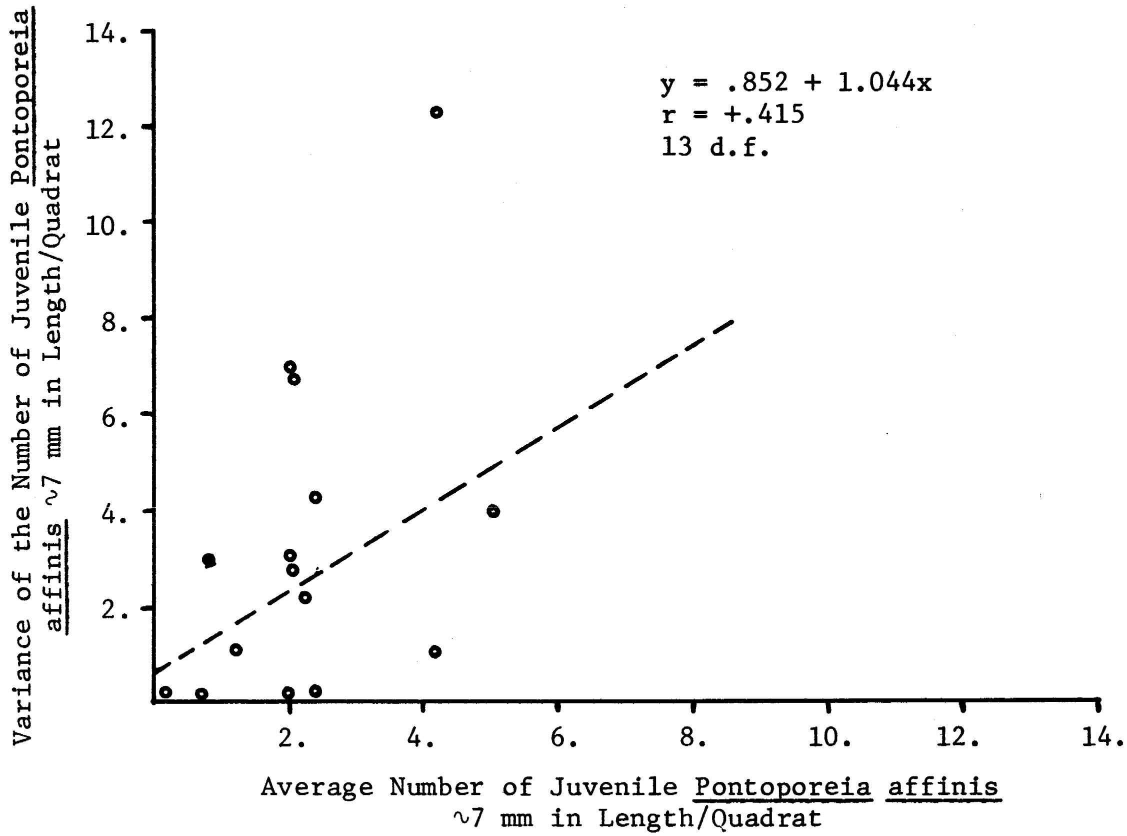


FIG. 17. The variance-mean relationship of juvenile <u>Pontoporeia affinis</u>, ~7mm in length per quadrat, from the short-term study area.

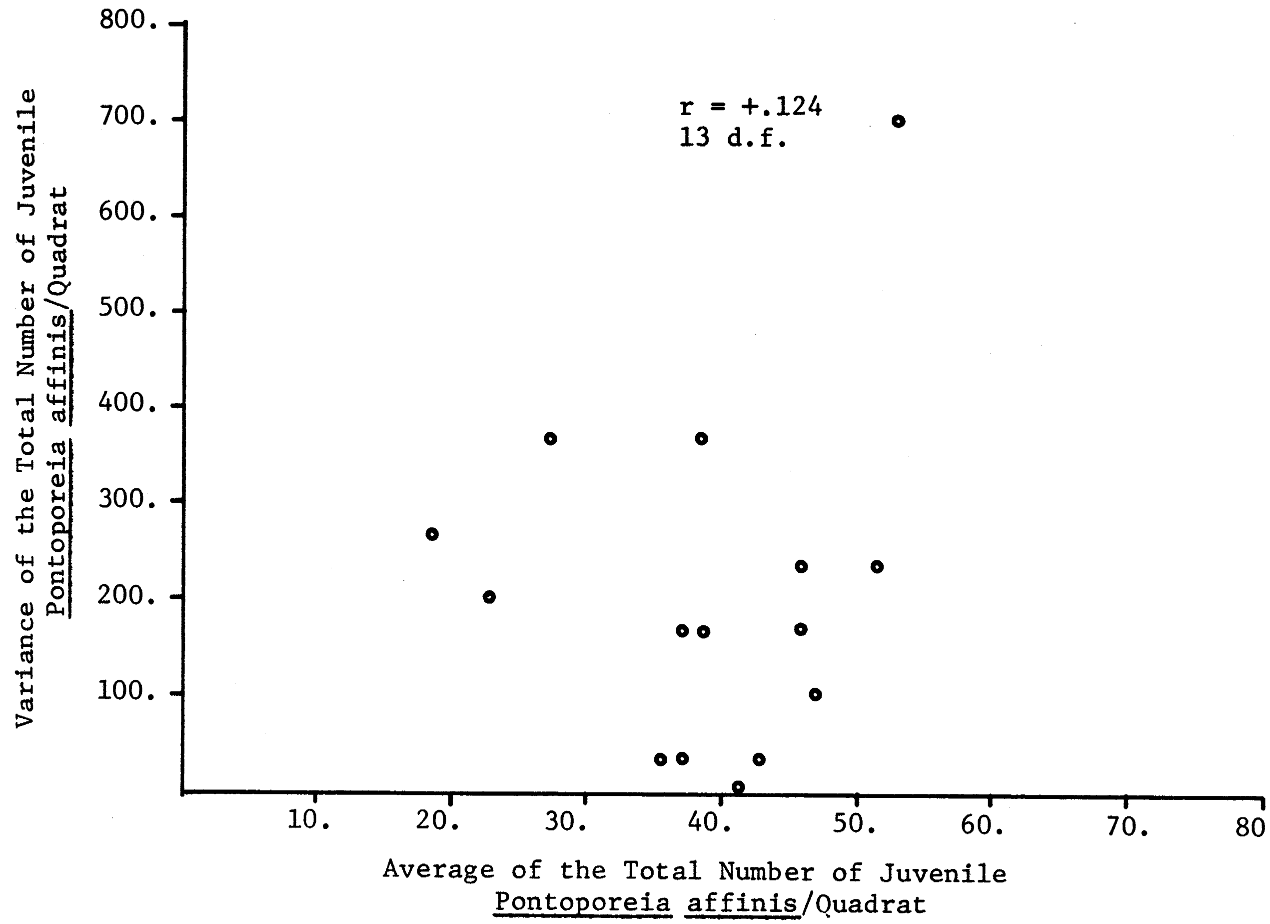


FIG. 18. The variance-mean relationship of the total number of juvenile *Pontoporeia affinis* of the short-term study area.

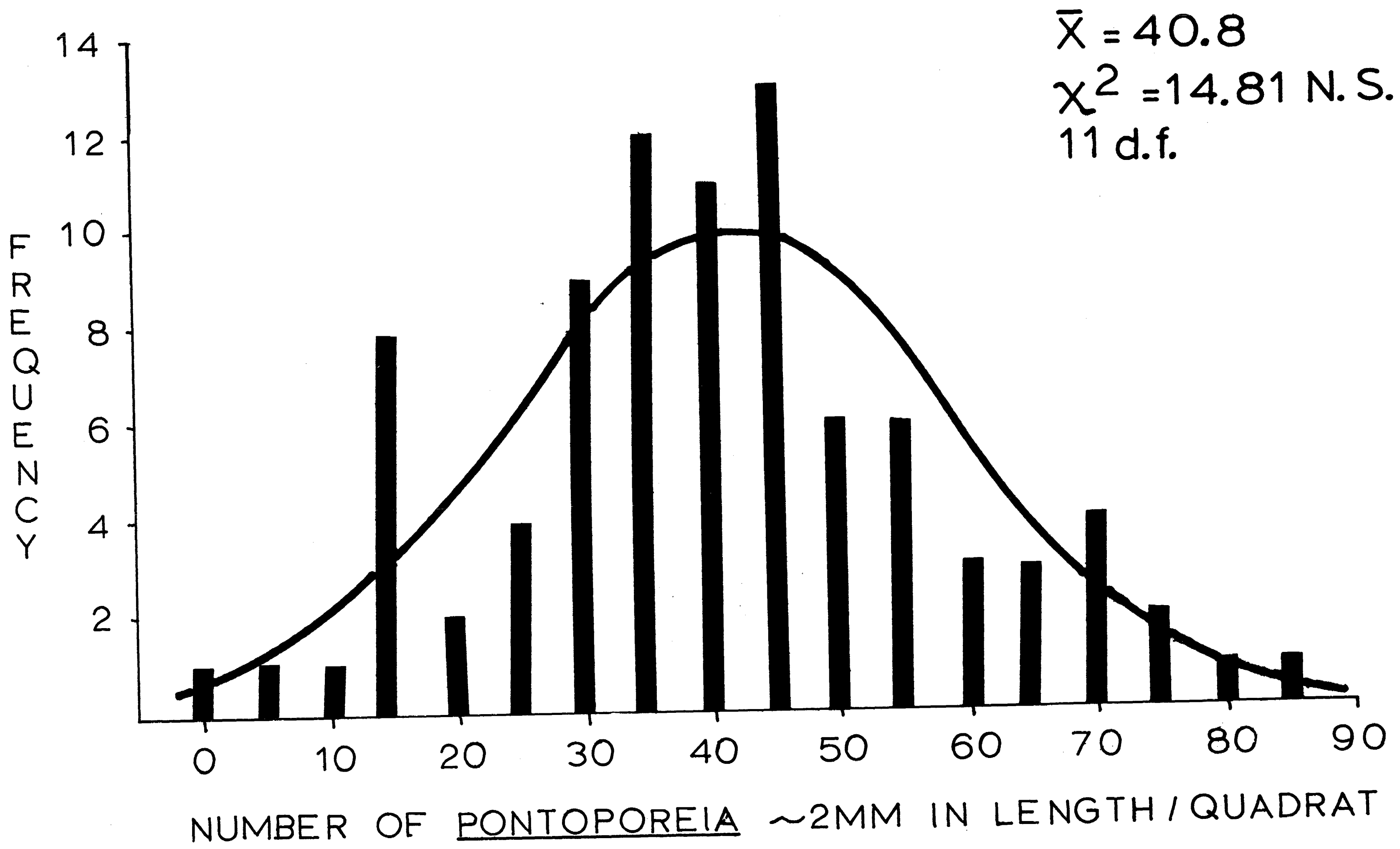


FIG. 19. The occurrence frequency histogram of Pontoporeia affinis. ~2 mm in length per quadrat, of the short-term study area superimposed on a normal distribution curve with the same mean and variance.

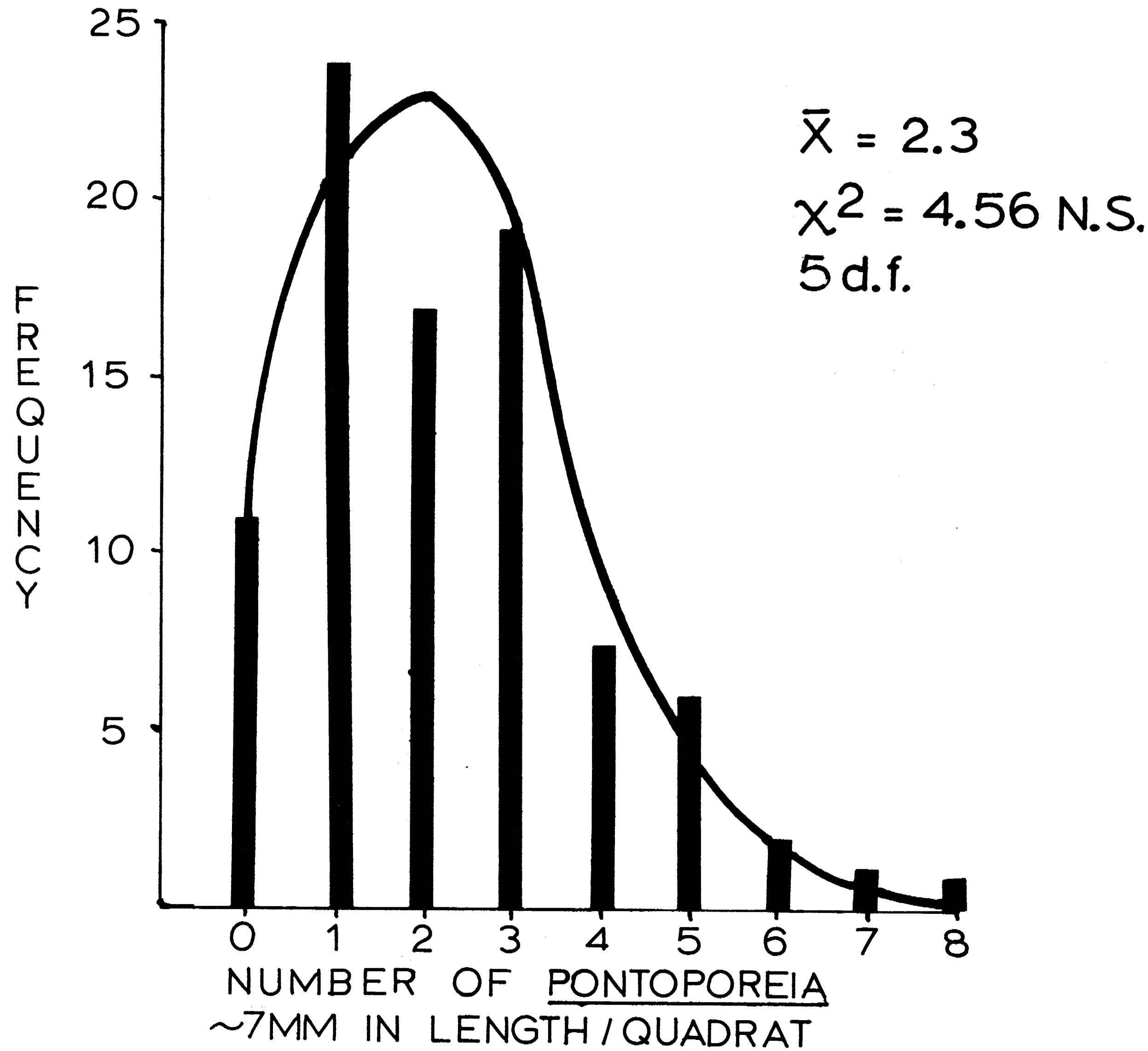


FIG. 20. The occurrence frequency histogram of *Pontoporeia affinis*, ~7 mm in length per quadrat, of the short-term study area superimposed on a Poisson series with the same mean.

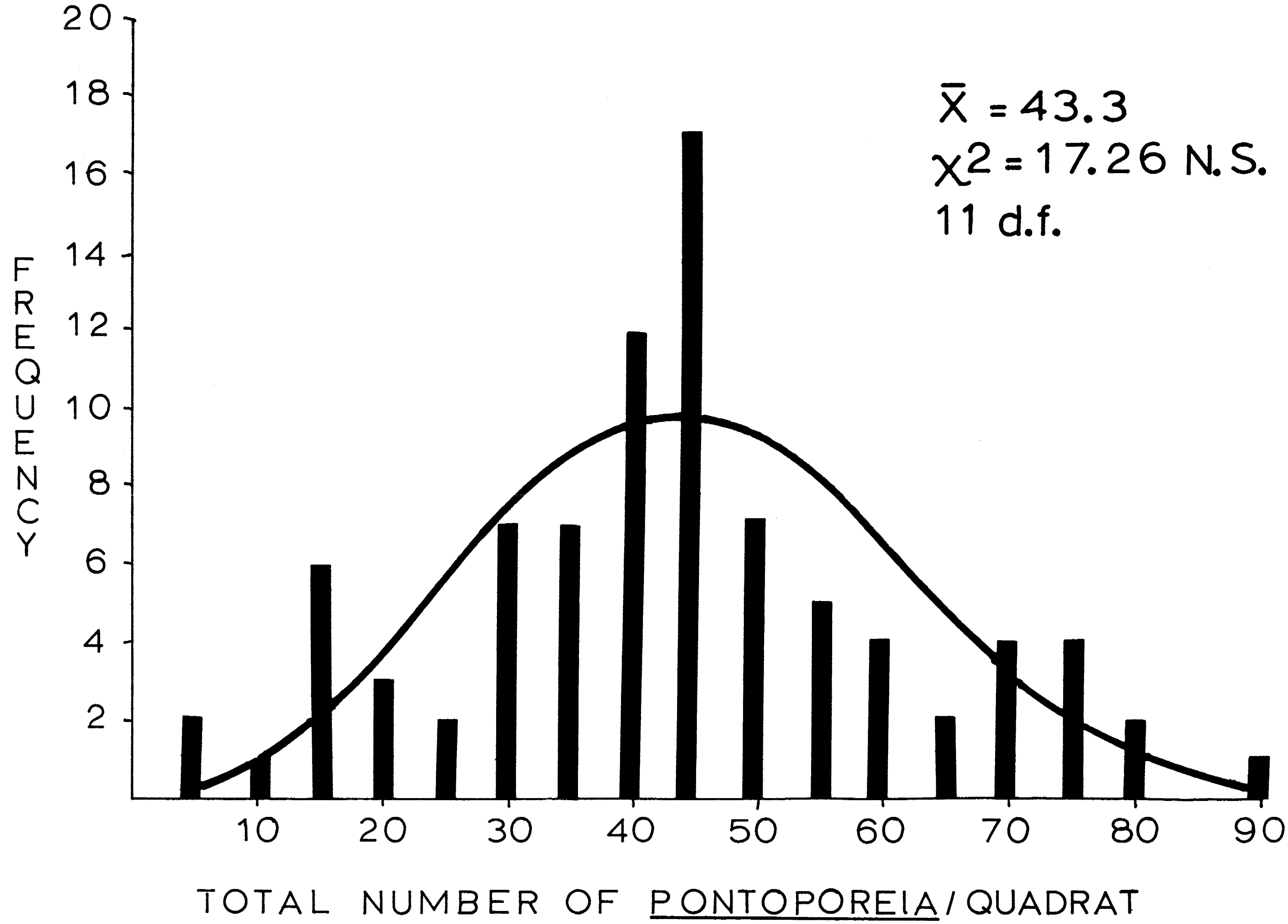


FIG. 21. The occurrence frequency histogram of the total number of juvenile Pontoporeia affinis of the short-term study area superimposed on a normal distribution curve with the same mean and variance.

bution. The theoretical curve for the normal distribution was calculated for small and total Pontoporeia utilizing the equation: $m = (N\,i / S\sqrt{2\pi})\,e^{-(X-\bar{X})^2/2S^2}$. The theoretical curve for the Poisson distribution was calculated for large Pontoporeia by: $m = Ne^{-\bar{X}}(1,\ X,\ \bar{X}^2/2!,\ \bar{X}^3/3!, \ldots \bar{X}^j/j!)$. In the above equations N represents the number of observations, $\bar{X}$ the average number of amphipods per category, i the size of the class interval, S^2 the variance, S the standard deviation, e the base of the natural logarithm, and m the expected number of individuals in an interval. The theoretical curves were superimposed on their respective histograms.

The chi square test for goodness of fit comparing the theoretical values with the observed values was calculated for each amphipod category. Because the probability of occurrence is exceedingly slight at the extreme ends of these curves and the 88 samples were not enough to represent adequately the distal areas of these curves, it was necessary to pool the extreme observed and expected values. The terminal intervals of the observed and expected values for each tail were combined until their sum approximated 3 organisms for the combined intervals. The following intervals were combined: 0-10 and 75-85 for small amphipods, 6-8 for large amphipods, and 0-10 and 75-85 for total amphipods.

In computing the normal distribution curves, the mean and standard deviation were estimated, thus the degrees of freedom for these curves are k - 3 where k represents the number of intervals. One degree of freedom is lost in estimating the chi square distribution. The degrees

of freedom for the small and total Pontoporeia are 11. Only the mean was estimated in calculating the Poisson distribution so the degrees of freedom for this curve are k - 2. The degrees of freedom for large Pontoporeia are 5. In every case the chi square test was not significant, indicating that the observed histograms did not deviate significantly from the expected distribution.

Long-Term Study Area

The mean and variance of the replicated samples taken at the 35 stations of the long-term study area were plotted against each other for total Pontoporeia per square meter (r = .417, d. f. = 575) (Fig. 22). The correlation coefficient computed for this plot implied a significant interaction between the mean and variance. The square root transformation was calculated for the data from every station stop. The mean and variance of these transformed data were plotted against each other (r = .076, d. f. = 573) (Fig. 23) and the mean appeared to be independent of the variance. The cube root and logarithmic transformations were also calculated for these data but the resulting correlation coefficients of the mean-variance relationship were significant. These results indicated that the square root transformation best removed the interaction that existed between the mean and variance.

On the other hand, the cube root transformation best removed the interaction that existed between the means and variances of the oligochaetes, sphaeriids, and chironomids. Transformed data have been

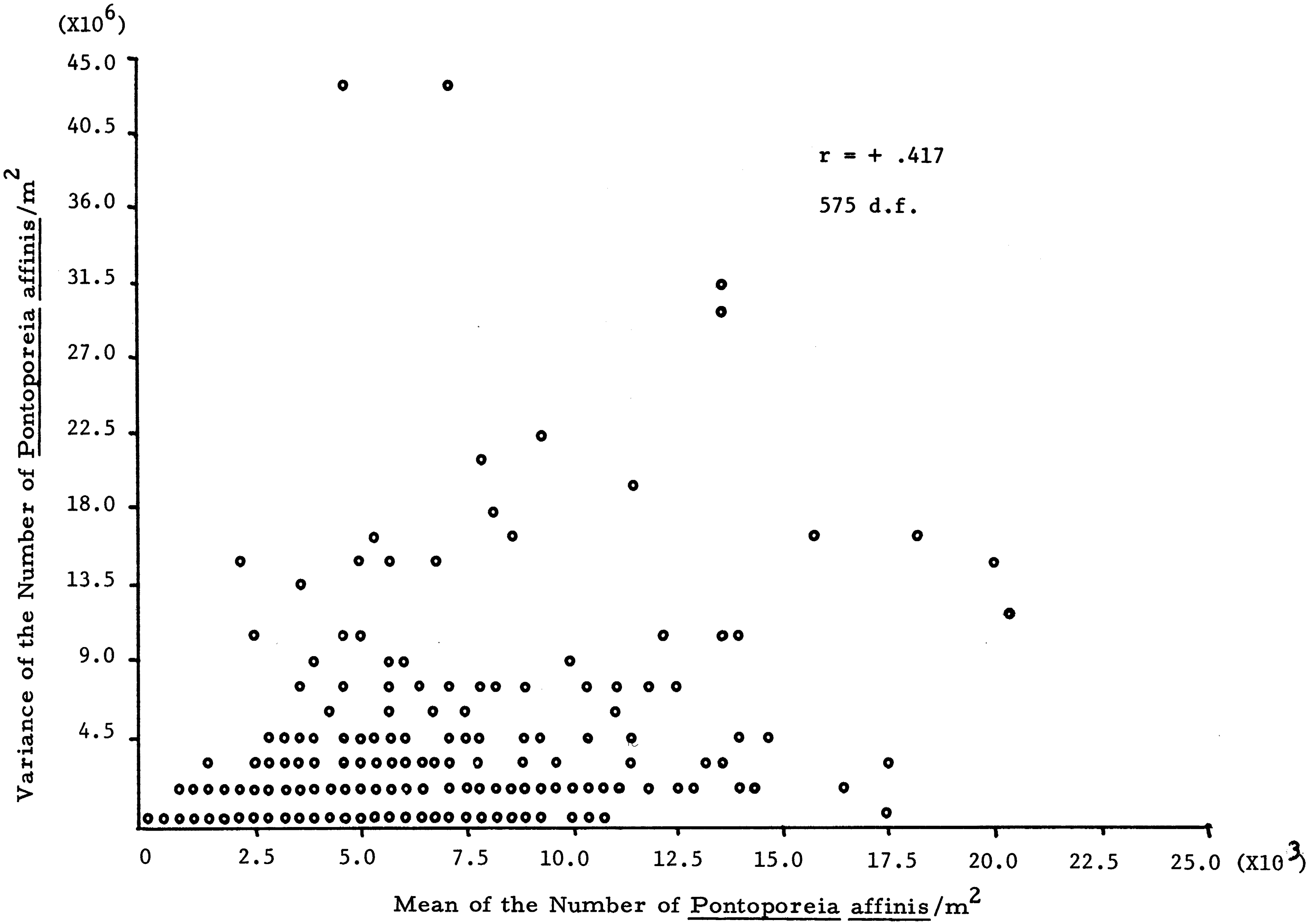


FIG. 22. The variance-mean relationship of the replicated samples of <u>Pontoporeia affinis</u> per square meter of the long-term study area.

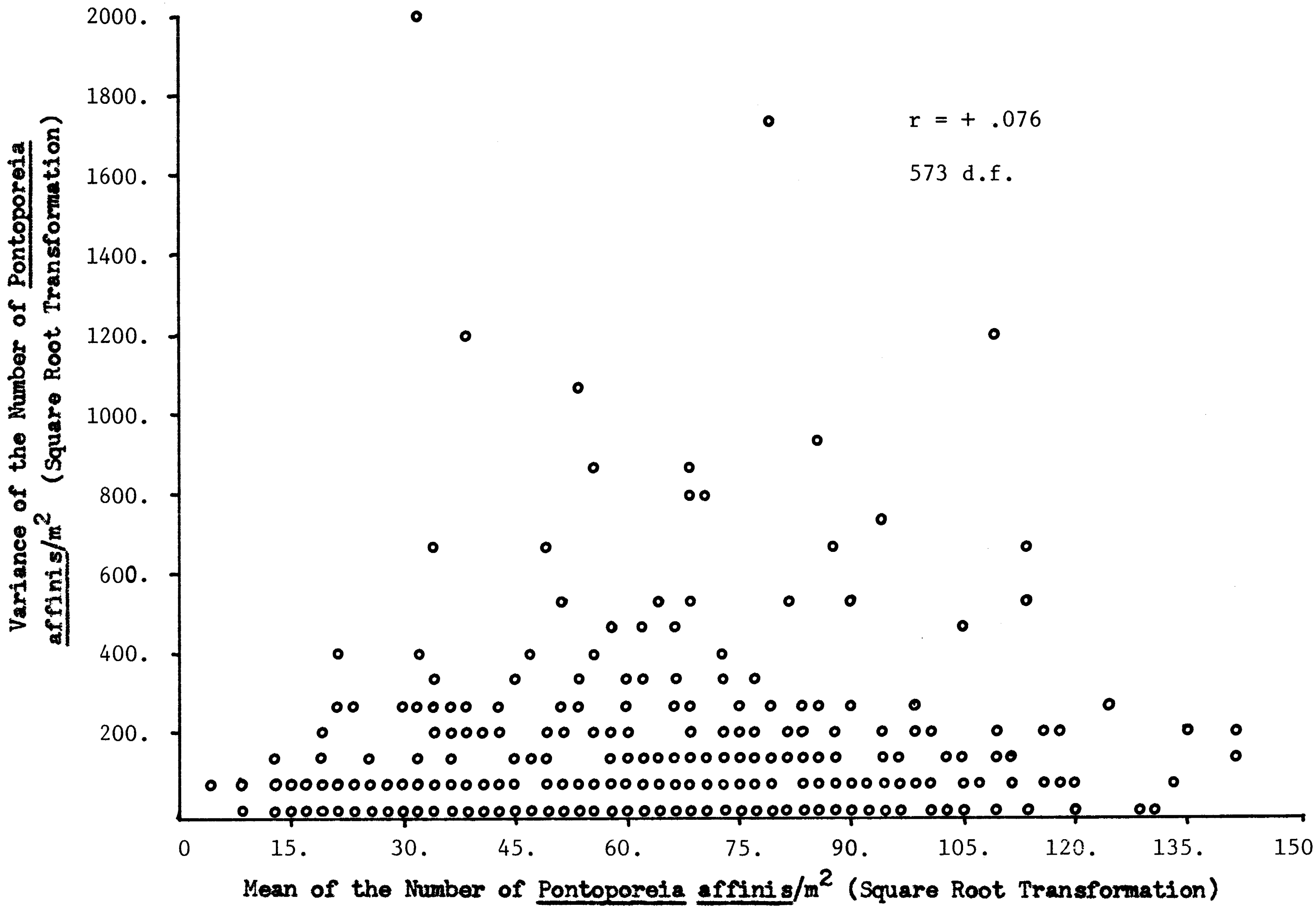


FIG. 23. The variance-mean relationship of the replicated samples of Pontoporeia affinis per square meter of the long-term study area (square root transformation).

used in the statistical treatment of the data collected at the stations of the long-term study area.

INTERSPECIFIC AND INTRASPECIFIC ASSOCIATIONS

The associations between Pontoporeia and the other macrobenthic groups of the short-term study area were determined by the correlation coefficients. The two size categories of this amphipod were treated independently of each other in the association analysis. Figure 24 indicates a significant association between small and large Pontoporeia; while figures 25 and 26 indicate that both small and large Pontoporeia exhibit a significant inverse relationship with the oligochaetes. Figure 27 shows a significant inverse relationship between large amphipods and the Sphaeriidae. Correlation analysis did not show significant associations between small amphipods and sphaeriids nor did it reveal significant relationship between this amphipod and the Chironomidae.

The associations between total Pontoporeia and the other macrobenthic groups of the long-term study area were also determined by correlation coefficients. Figures 28-30 indicate that total Pontoporeia were positively associated with oligochaetes, sphaerids, and chiromonids.

ENVIRONMENTAL RELATIONSHIPS

For this investigation it was assumed that Pontoporeia responds to changes in its environment and that these changes are reflected by increases or decreases in abundance. A low density indicates response

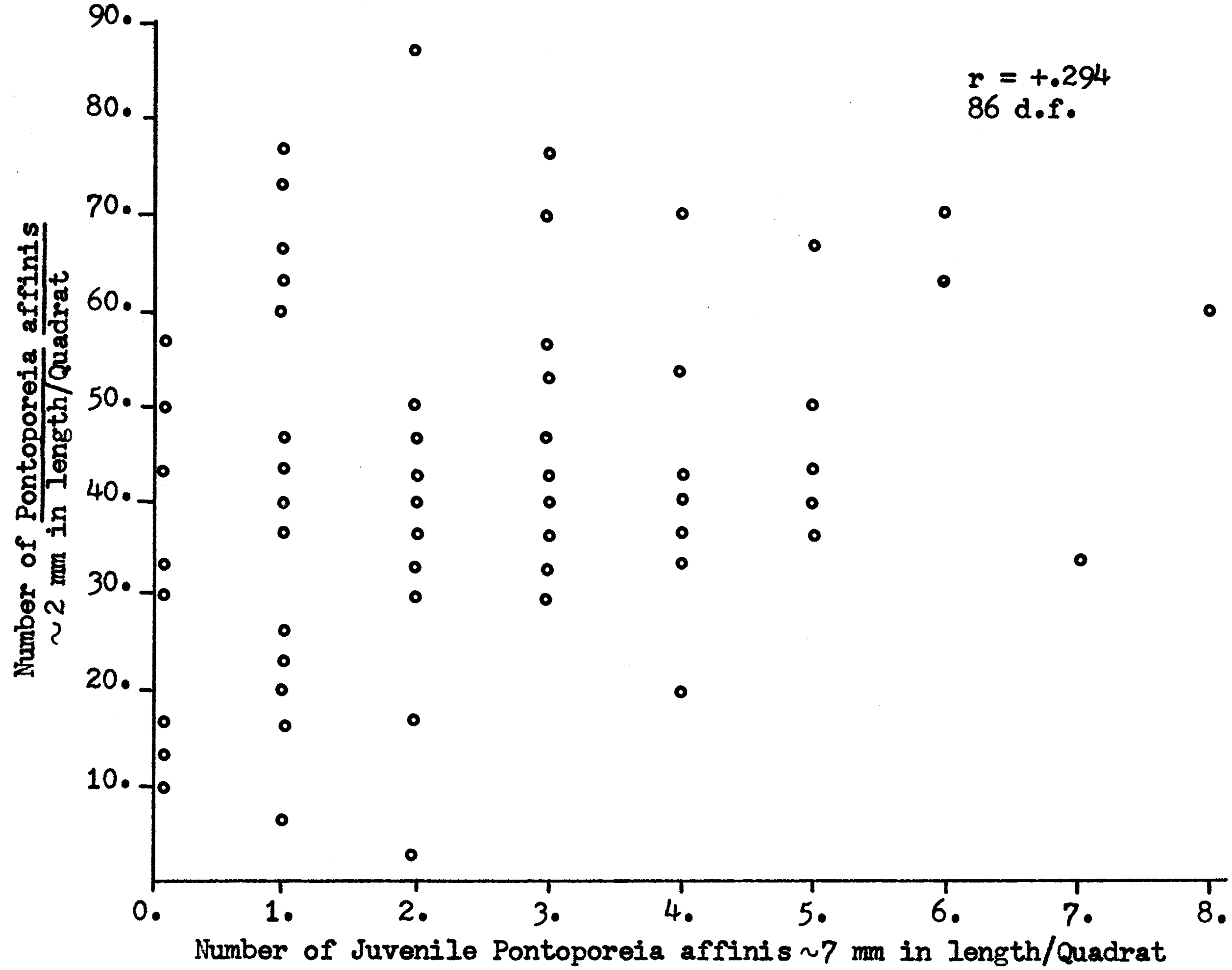


FIG. 24. Association of large and small juvenile Pontoporeia affinis of the short-term study.

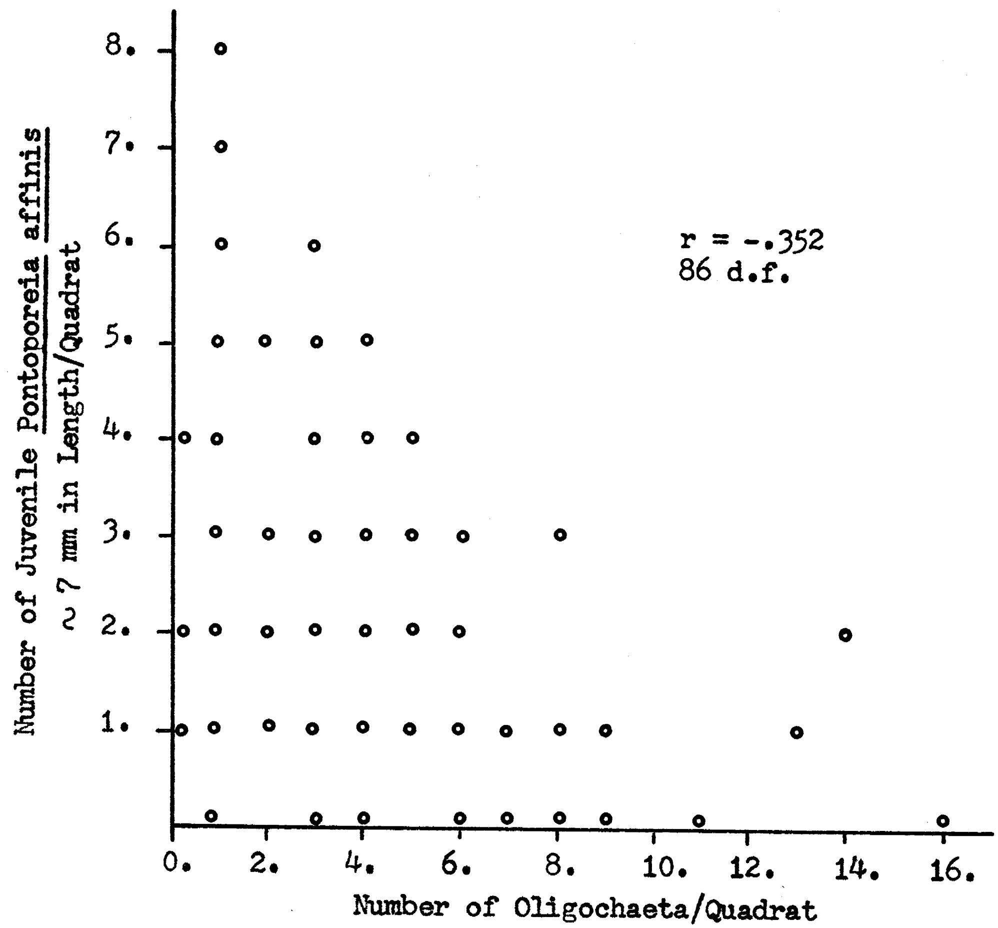


FIG. 25. Association of juvenile Pontoporeia affinis ∼7 mm in length and Oligochaeta of the short-term study area.

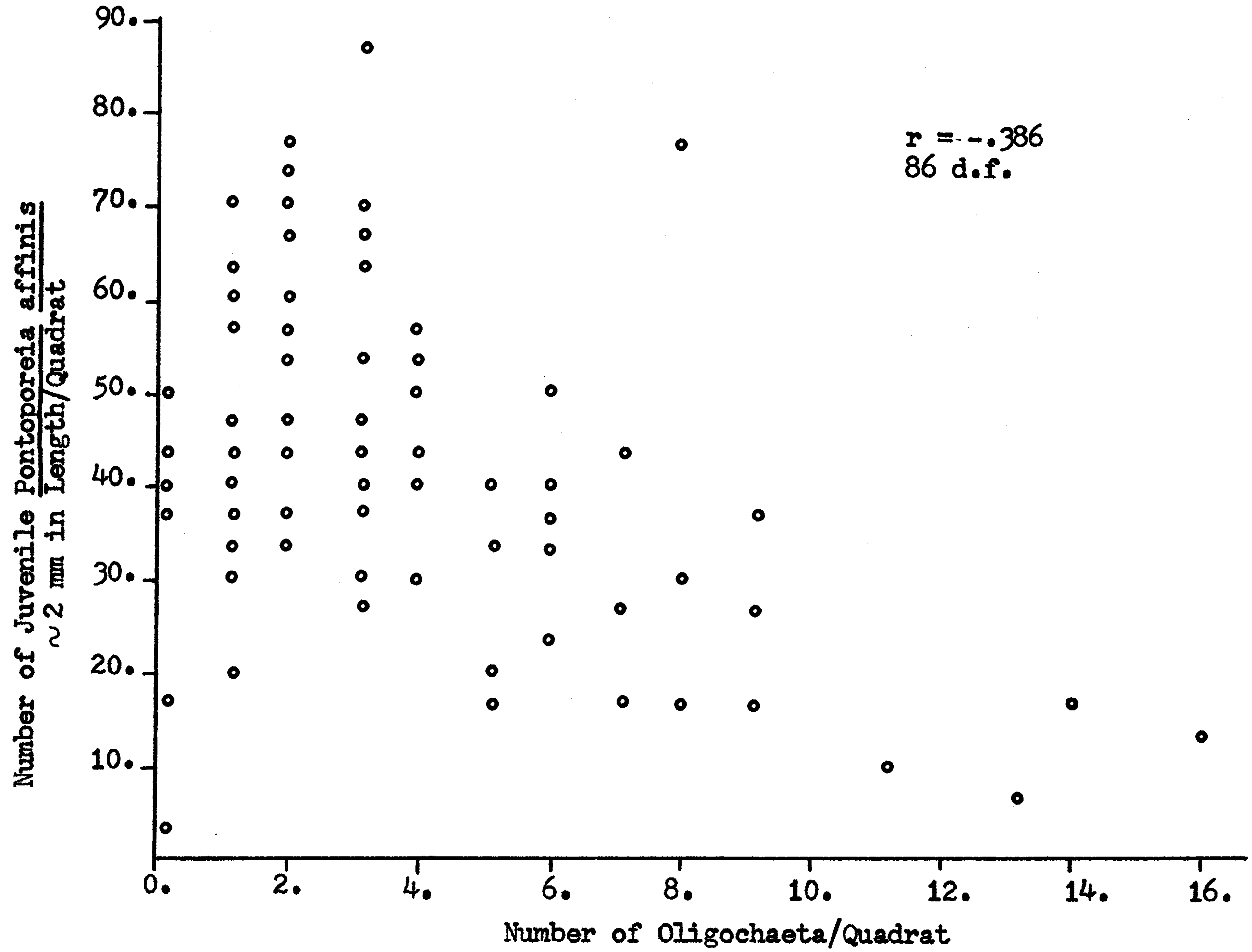


FIG. 26. Association of juvenile Pontoporeia affinis ~2 mm in length and Oligochaeta of the short-term study area.

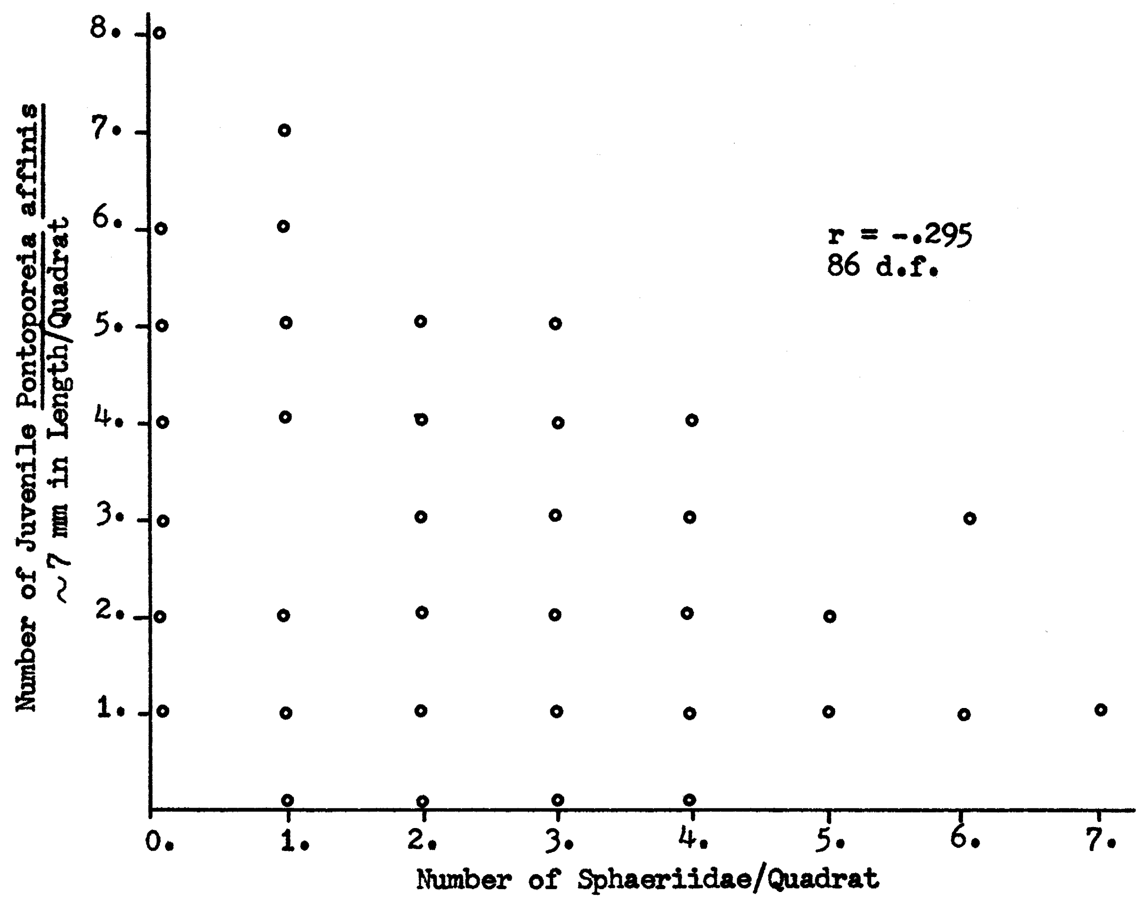


FIG. 27. Association of juvenile <u>Pontoporeia</u> <u>affinis</u> ~7 mm in length and Sphaeriidae of the short-term study area.

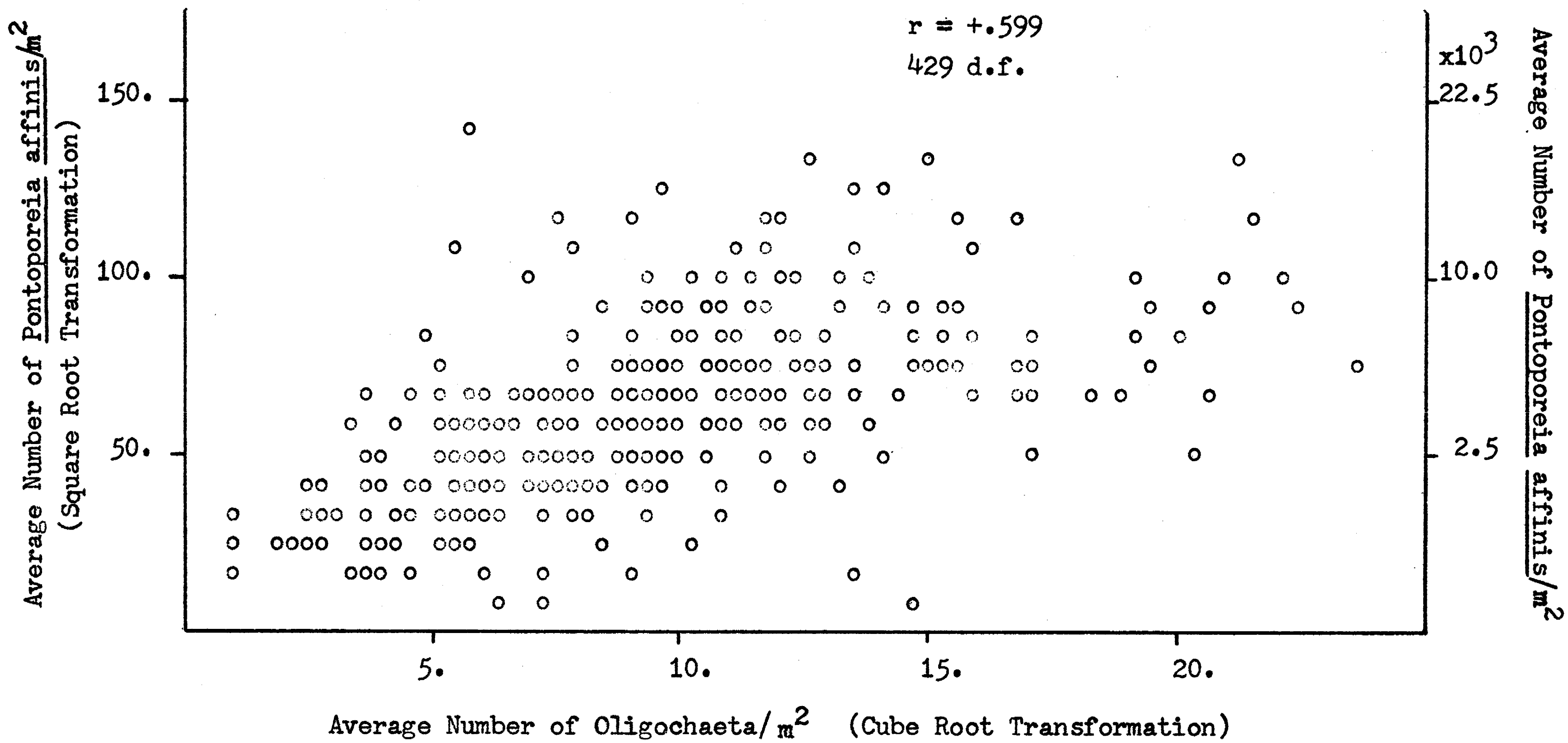


FIG. 28. Association of Pontoporeia affinis and Oligochaeta of the long-term study area.

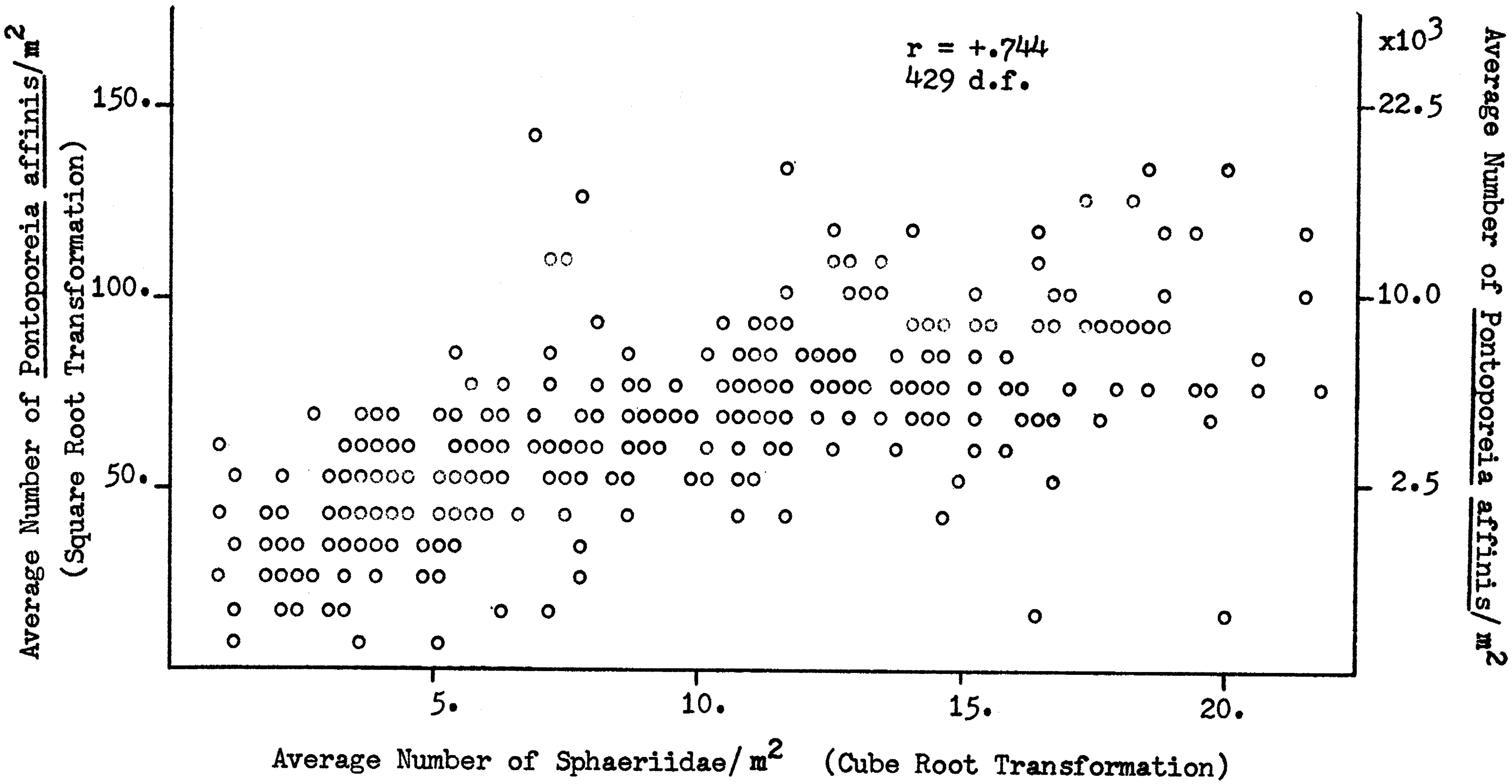


FIG. 29. Association of Pontoporeia affinis and Sphaeriidae of the long-term study area.

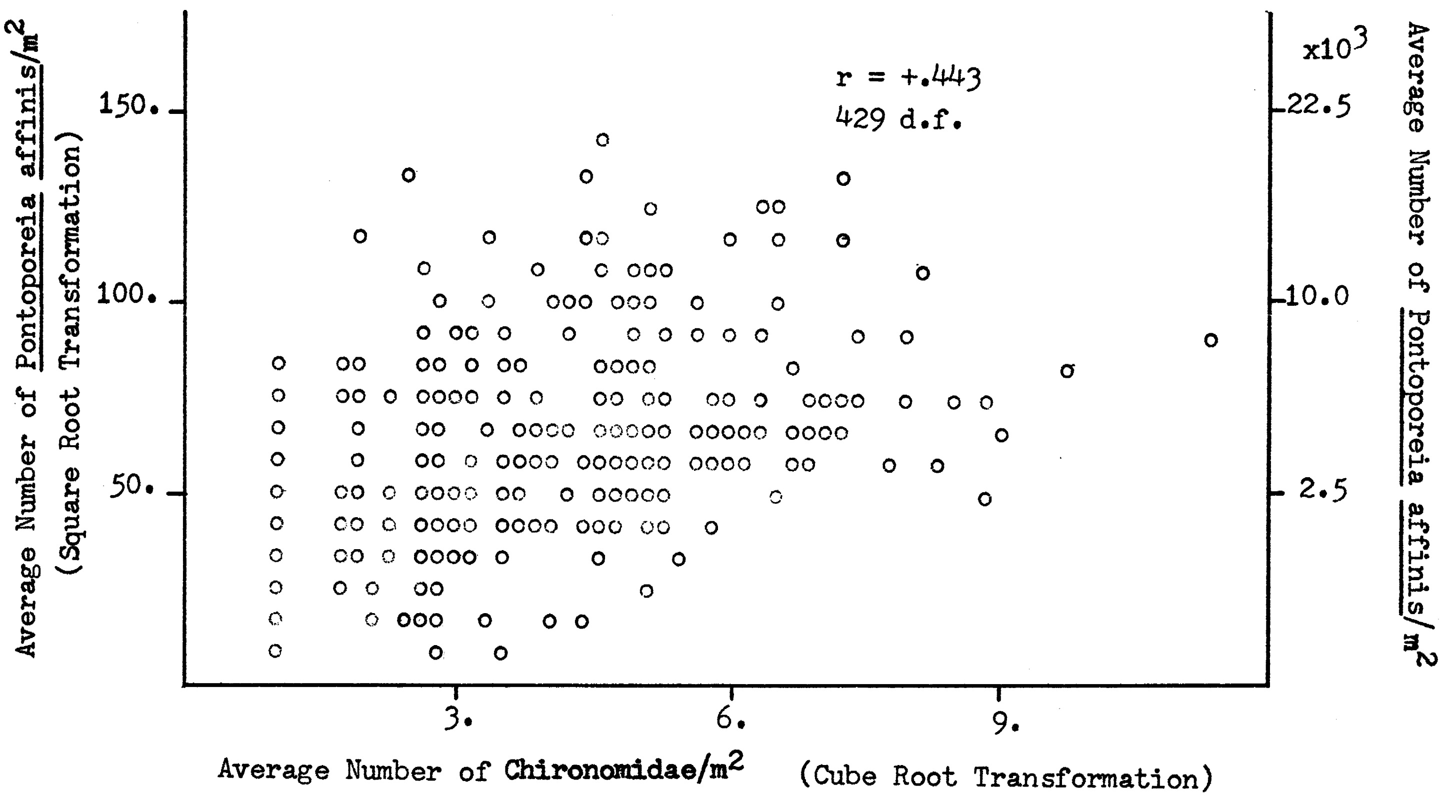


FIG. 30 Association of Pontoporeia affinis and Chironomidae of the long-term study area.

to the environment in a negative fashion while a high density represents a positive environmental response. Data collected from 35 stations of the long-term study area were used in examining these environmental relationships.

The data were analyzed by three methods. In the first an environmental factor, such as depth, was divided into increments and a geometric mean calculated for the combined amphipod counts of each interval. The geometric mean of each interval was accompanied by an upper and lower limit of one standard deviation unit. In the second method a correlation coefficient was computed by comparing the average density of Pontoporeia with an environmental parameter. Stepwise multiple linear regression was used as the third method of investigating these relationships. The effects of environmental factors on changes of amphipod density are considered simultaneously in this method of analysis.

The geometric mean is usually calculated by $(X_1 . X_2 . X_3 . \ldots X_j)^{1/j}$ where X_1 represents a sample of amphipod counts. Counts in this analysis were converted into logarithms with the geometric mean being determined from the antilog of $\log X_1 + \log X_2 + \log X_3 + \ldots \log X_j)/j$. The upper and lower limits of this mean were determined by first computing the standard deviation of the log converted data, adding this standard deviation to and subtracting it from the long mean, and the antilogs of these two values finally constituting the upper and lower limits.

The geometric mean was used because it is a more conservative estimate of the theoretical mean and is not affected by extreme values to the same extent as the arithmetic mean. The geometric mean also gives smaller counts relatively more importance than they enjoyed in the computation of the arithmetic mean. The upper and lower limits were calculated in the previously described manner because this method eliminates the possibility of negative confidence intervals.

The correlation coefficient was employed as the second method of analysis because it is a useful tool for measuring the degree of a relationship. The computer program written to compute the correlation coefficient was also designed to present the relationship graphically. The computer automatically rounded off the results in the construction of the graph so these values are printed in regularly spaced columns and rows. It is impossible to interpret the relative importance of these data points because each point may actually represent more than one value. These graphs merely show the trends of the relationships while the correlation coefficients indicate the degree of the relationship.

The third method, that of multiple linear regression, is a useful statistical tool in the study of biological systems because it has the ability of mathematically removing the effects of confounding environmental factors. Stepwise multiple regression analysis has the additional feature of generating the multiple regression equation, variable by variable, in the order of their relative importance.

The general multiple regression equation is written $Y = a + b_1X_1 + b_2X_2 + \ldots b_jX_j$ where X_1 represents an independent variable such as depth, b_1 the regression coefficient, a the intercept, and Y the dependent variable. The dependent variable in this study is the density of *Pontoporeia*/m^2 while the independent variables include surface and bottom temperature, depth, depth squared, sediment type, day of the year, percent carbon in the sediment, distance from shore, and the densities of oligochaetes, sphaeriids, and chironomids.

An initial examination of the depth distribution of *Pontoporeia* (Fig. 31) indicated this was a curvilinear relationship which could possibly be satisfied by a second order polynomial equation. Depth was squared and this value was treated as the additional variable that would possibly satisfy this curvilinear relationship. In another study involving the stations of the C, D, and E transects an additional parameter, wave height, was added to the previously discussed independent variables.

In the first section of the following analysis, a two dimensional presentation is made showing the effects of environmental parameters on the abundance of *Pontoporeia*. This is accomplished by comparing the geometric mean number of *Pontoporeia* with the environmental factors and also by examining the correlation coefficients of these relationships. Stepwise multiple regression analysis was employed in the second part of this section to show how the environmental factors, acting together, affect the quantity of *Pontoporeia*.

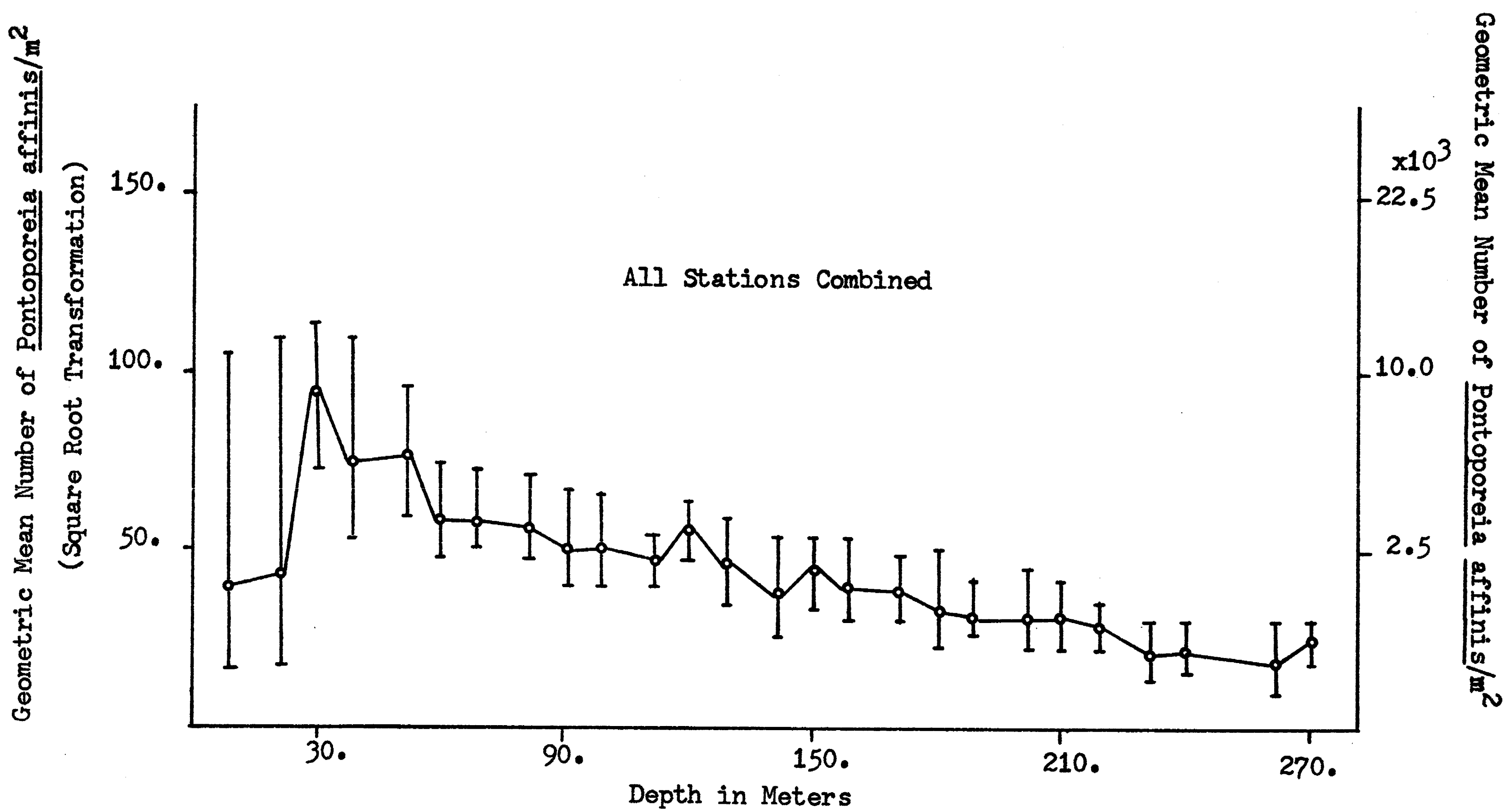


FIG. 31. Average number of Pontoporeia affinis per square meter pooled by 10 m depth increments.

Environmental Parameters Treated Individually

Depth: The samples of *Pontoporeia* were pooled into 10 m depth increments. The shallowest depth interval included all observations between 9 and 15 m and was designated the 10 m increment. The next depth interval, including all observations between 16 and 25 m, was the 20 m increment, and so forth. An inspection of Figures 31 and 32 shows that the maximum density of *Pontoporeia* occurred around the 30 m. On the average, there were fewer individuals at the 10 and 20 m than at 30 m and the confidence intervals show considerably more variability at these two depths than at any of the others. There is a sharp decline of amphipods from 30 to 40 m, then a leveling off from 40 to 50 m with another sharp decline from 50 to 60 m. They gradually decrease from 60 to 230 m, beyond which the density is fairly uniform. The correlation coefficient showed this same relationship.

Time: All observations of the three sampling seasons were combined into monthly intervals for *Pontoporeia* and no sighnificant monthly variation in abundance was found (Fig. 33). Figure 34 likewise indicates no significant correlation between average number of *Pontoporeia* per station stop and day of the year.

Bottom Temperature: The samples of *Pontoporeia* were pooled with respect to bottom temperature increments consisting of $1^{\circ}C$ intervals. The 1° interval included all observations between 0.6 and $1.5^{\circ}C$ while the 2° increment contained all observations between 1.6 and $2.5^{\circ}C$

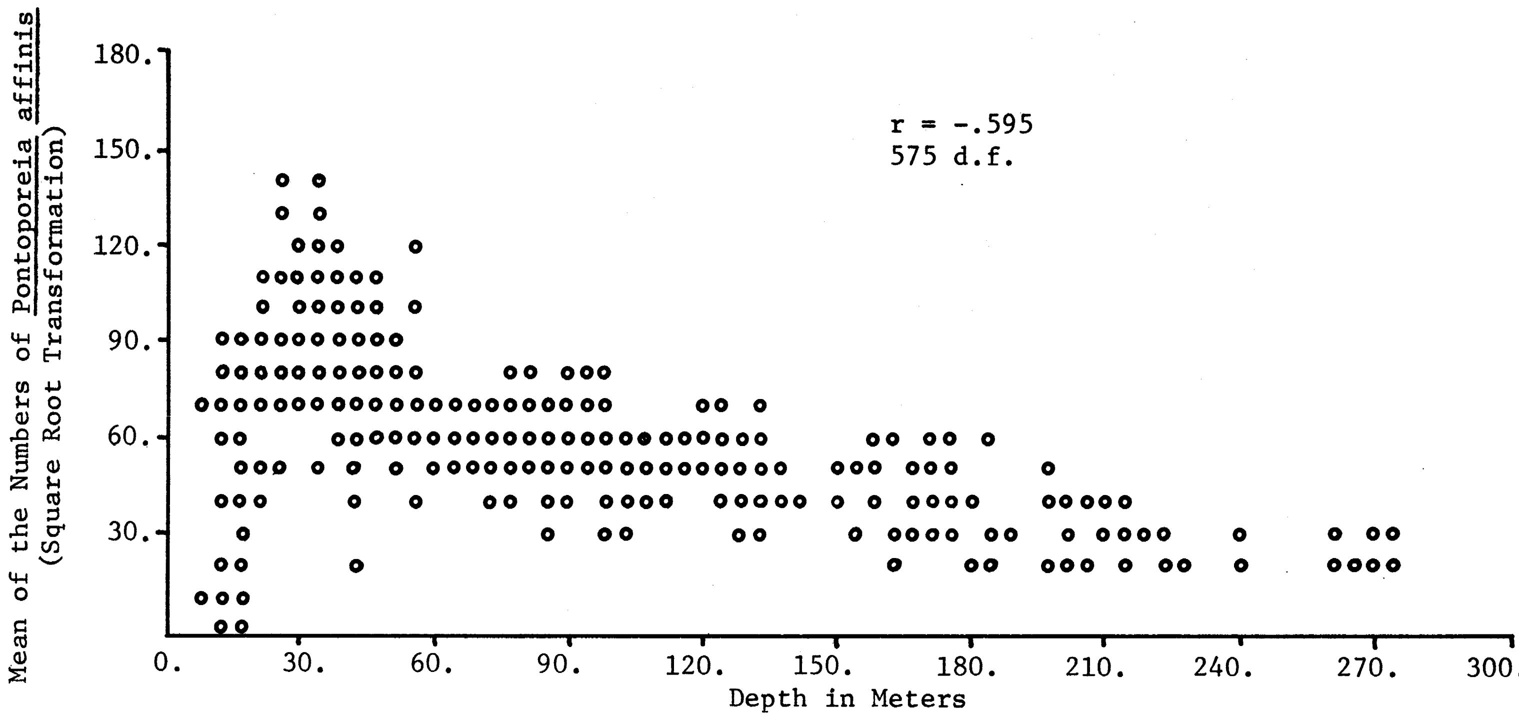


FIG. 32. Average number of Pontoporeia affinis per square meter obtained at each station visit versus depth in meters.

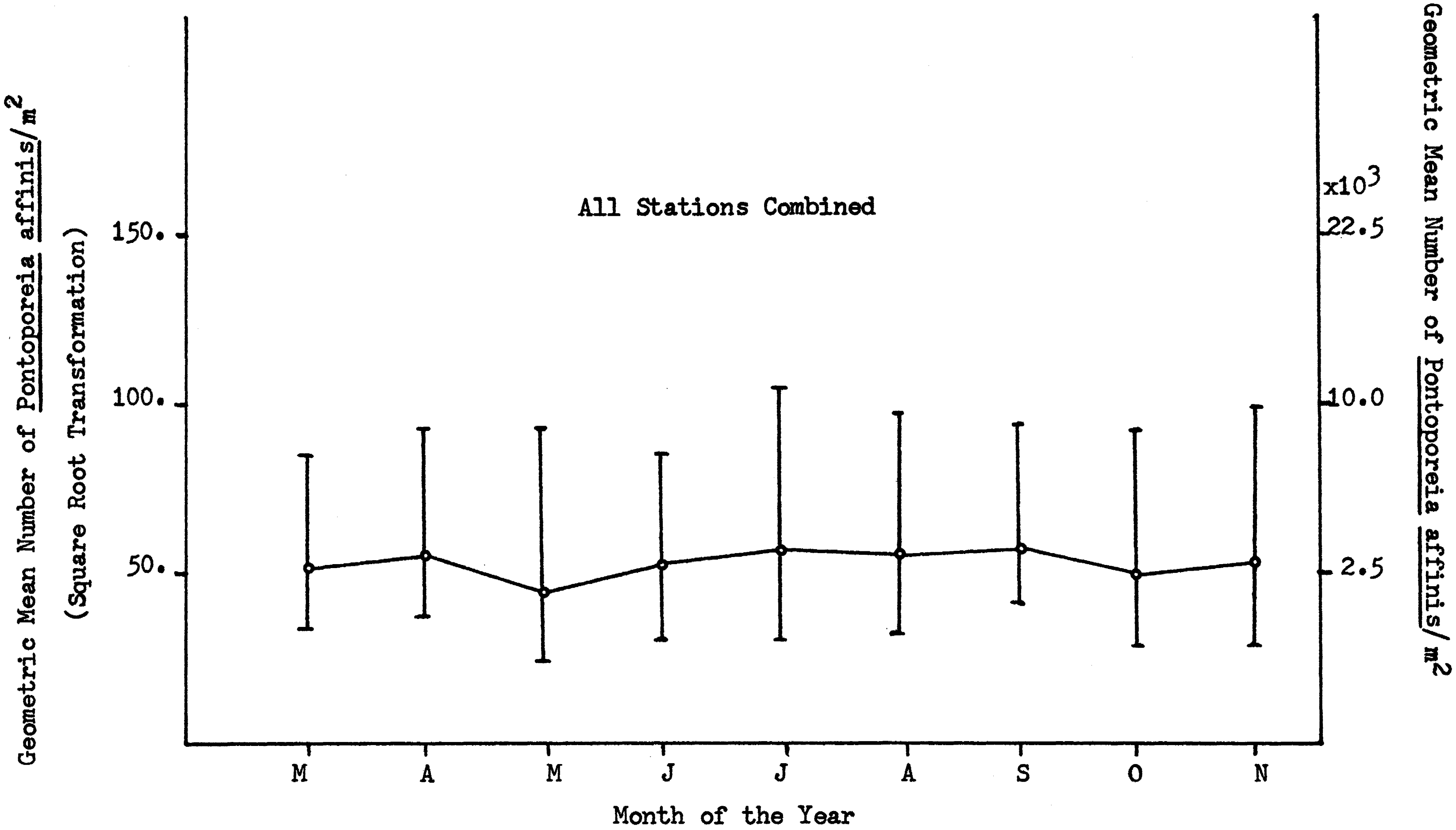


FIG. 33. Average number of <u>Pontoporeia</u> <u>affinis</u> per square meter pooled by monthly intervals.

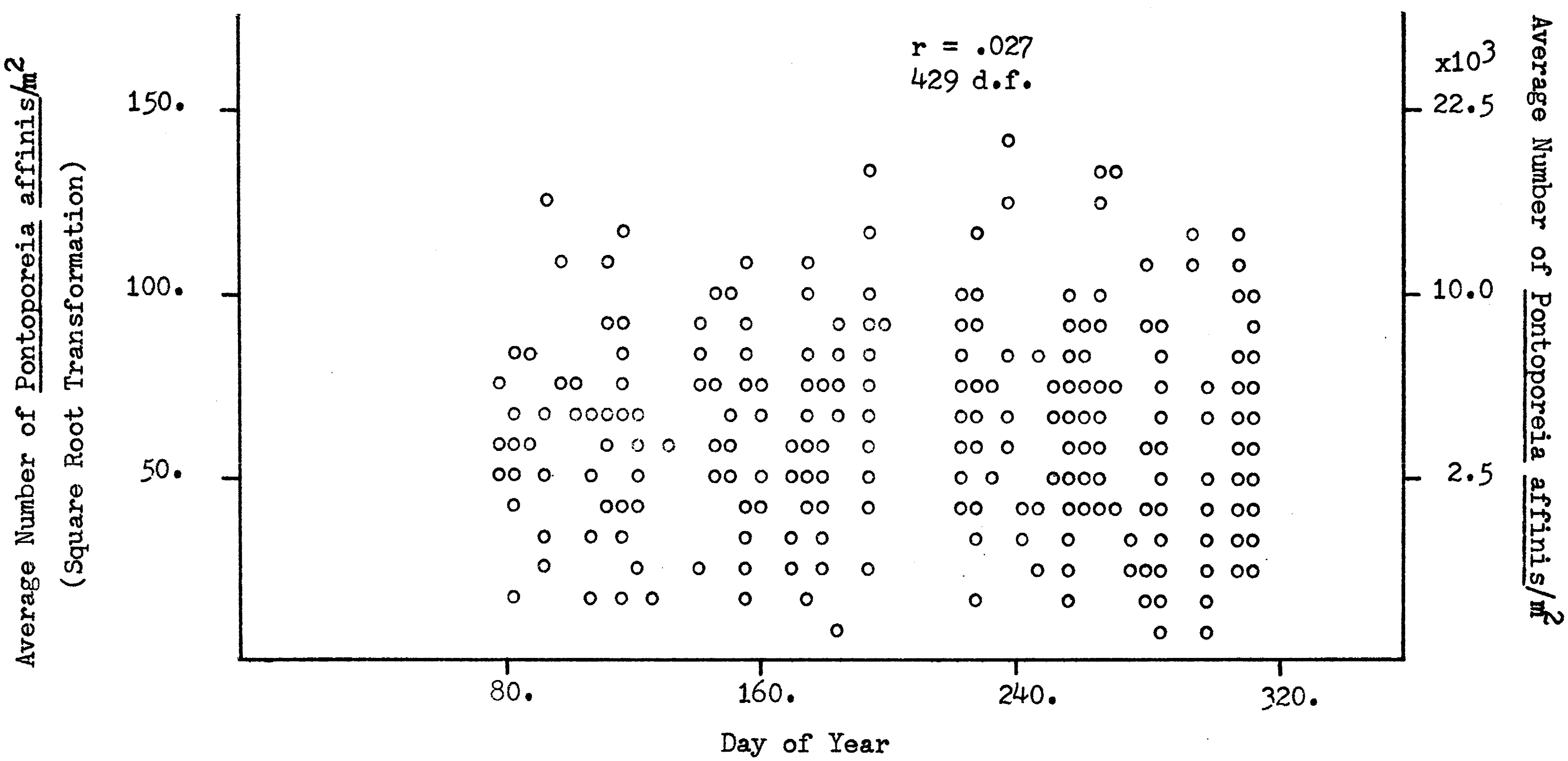


FIG. 34. Average number of Pontoporeia affinis per square meter obtained at each station visit versus day of year.

and so forth (Fig. 35). The extremely high value found at 16°C represents 3 observations from only one station stop. Although a positive correlation at the 1 percent level was obtained, the scatter diagram reveals that this is a very weak association (Fig. 36).

Sediment Type: In the statistical analysis, the sediment categories were ranked from one to five, with sand receiving a rank of 1, sandy silt a rank of 2, silt 3, layered 4, and hard bottom 5. Figure 37 indicates that *Pontoporeia* was most abundant in the sandy silt and was next most abundant in the sand sediments. Abundance was about the same in silt and layered sediments. It is not surprising that *Pontoporeia*, a burrowing amphipod, was least abundant in the hard bottom samples. Figure 38 shows the variability in amphipod density was much greater for the sand sediments, which probably reflects the fact that these sediments are found in the shallow inshore regions of the lake that are subjected to greater environmental extremes.

Percent Organic Carbon in the Sediment: The samples of *Pontoporeia* were pooled with respect to tenths of percent organic carbon in the sediment (Fig. 39). There is a definite increase in average abundance of *Pontoporeia* from 0.04 to 0.2 percent organic carbon. A general decline in density takes place from 0.2 to 1.6 percent with a sharp increase occurring at 1.7 percent. Density gradually decreased from 1.7 to 2.5 percent, followed by an increase at 2.7 percent, and a general decrease when organic carbon exceeded 2.7 percent. Figure 40 shows

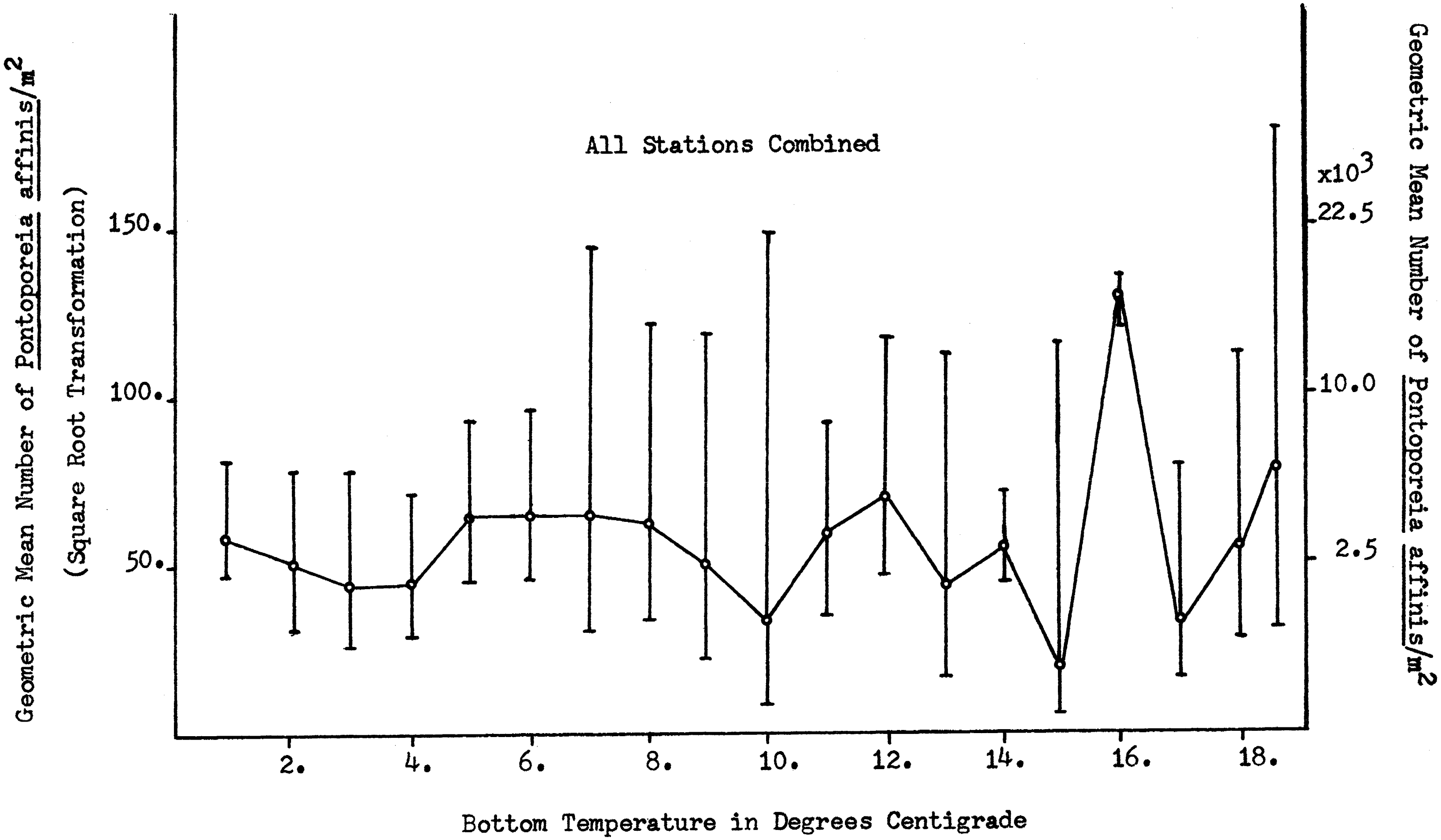


FIG. 35. Average number of Pontoporeia affinis per square meter pooled by one degree centigrade increments.

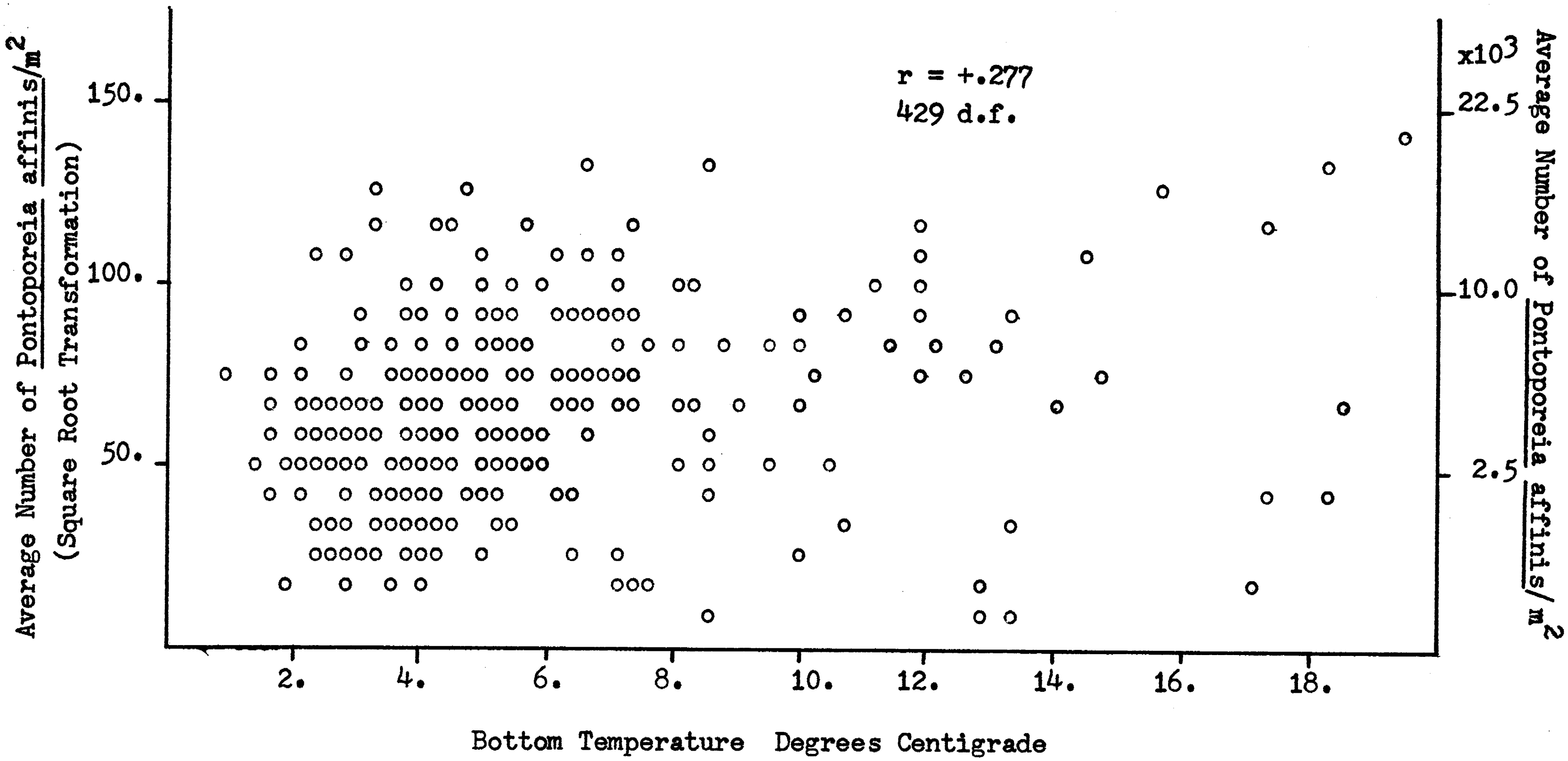


FIG. 36. Average number of Pontoporeia affinis per square meter obtained at each station visit versus bottom temperature in degrees centigrade.

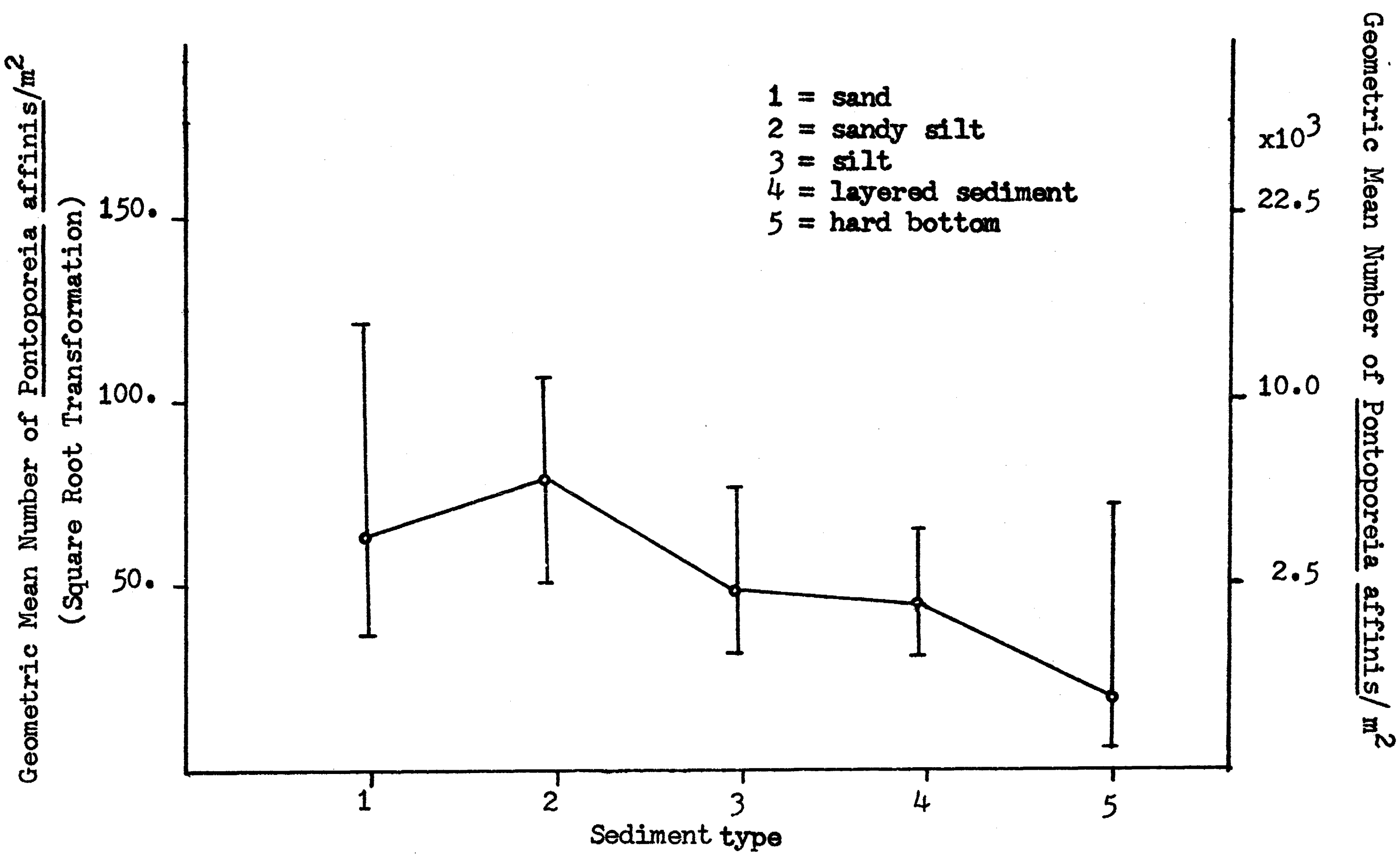


FIG. 37. Average number of Pontoporeia affinis per square meter pooled by sediment type.

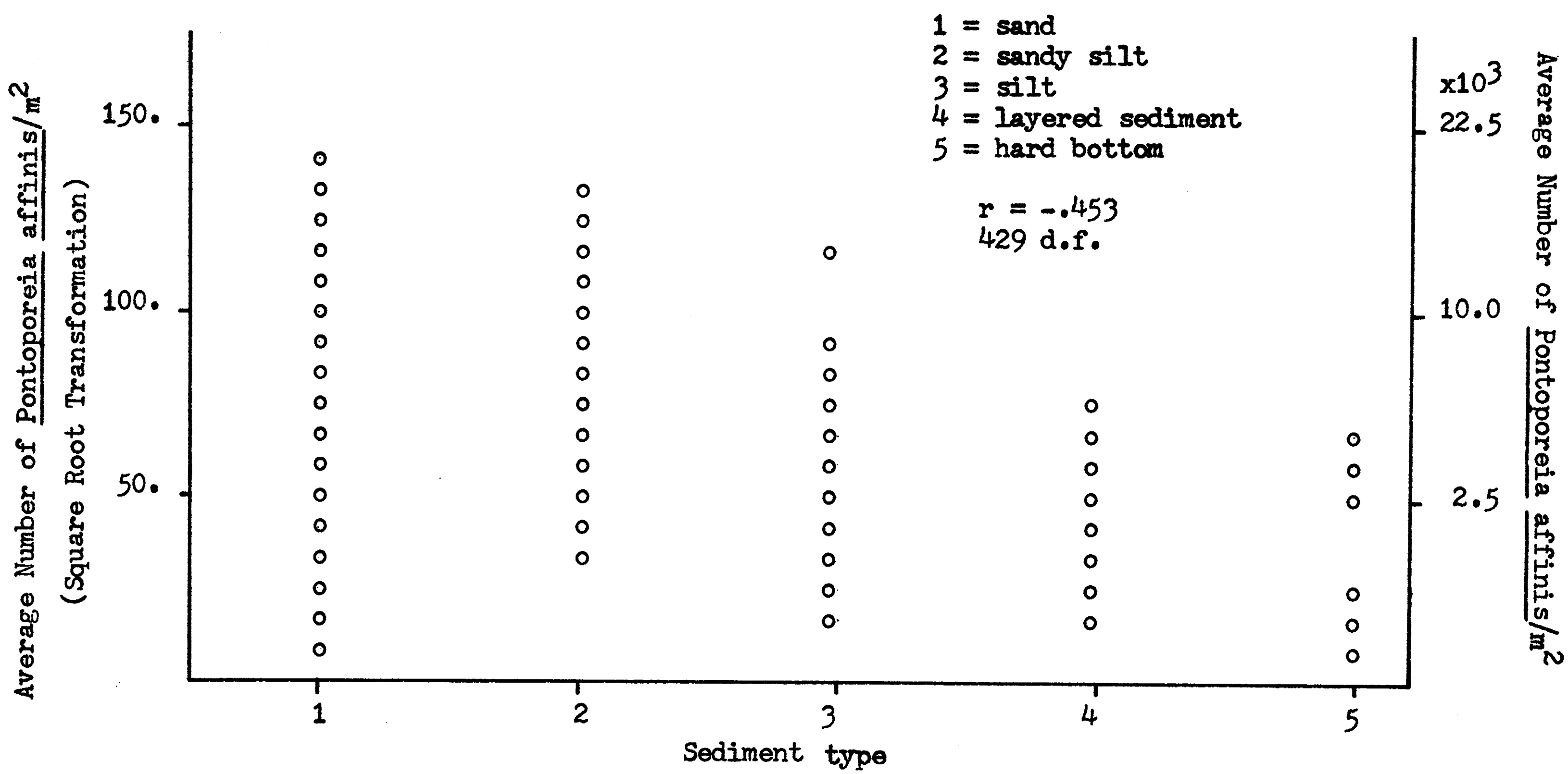


FIG. 38. Average number of Pontoporeia affinis per square meter obtained at each station visit versus sediment type.

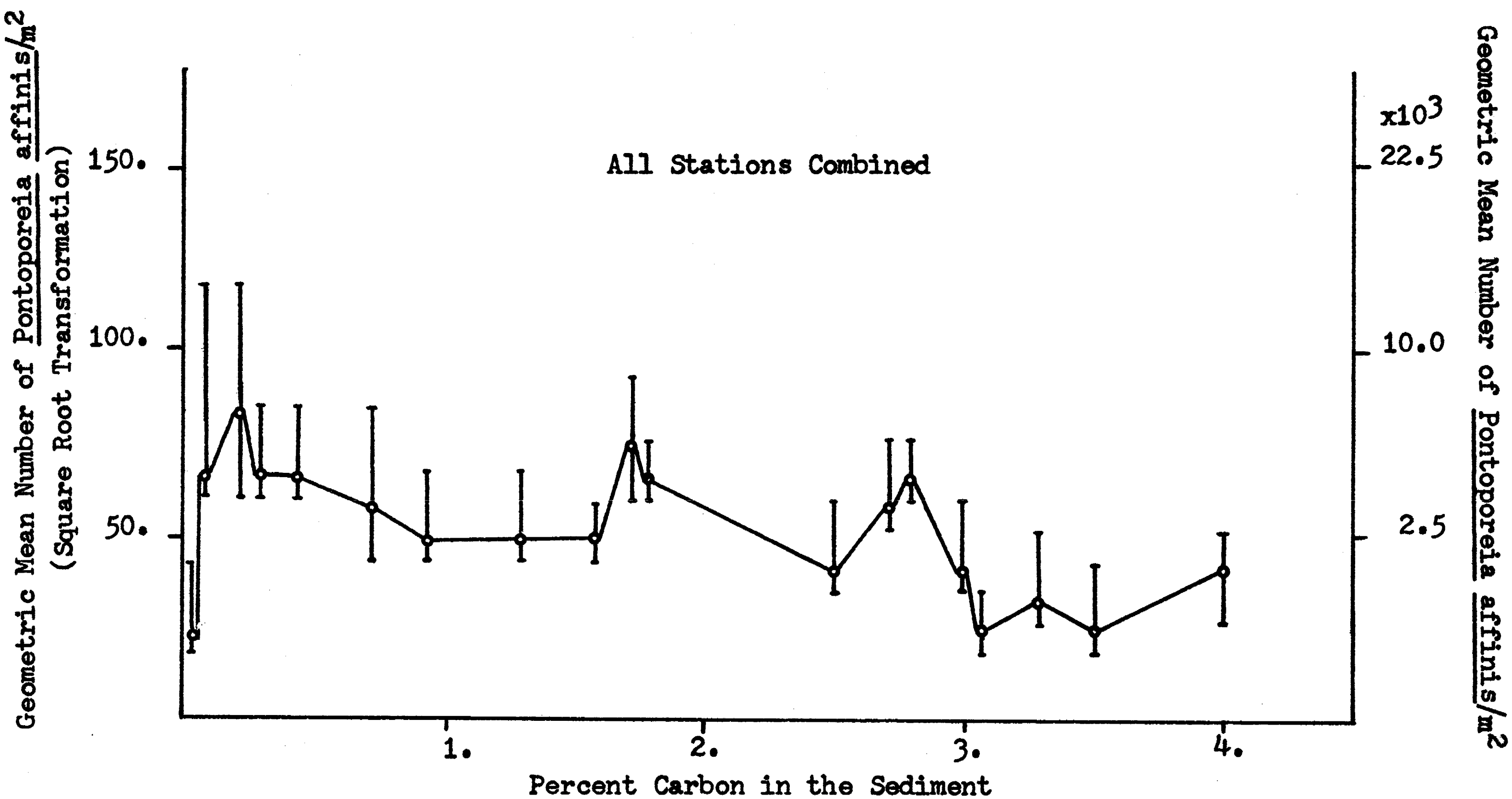


FIG. 39. Average number of Pontoporeia affinis per square meter pooled by tenths of a percent organic carbon in the sediment.

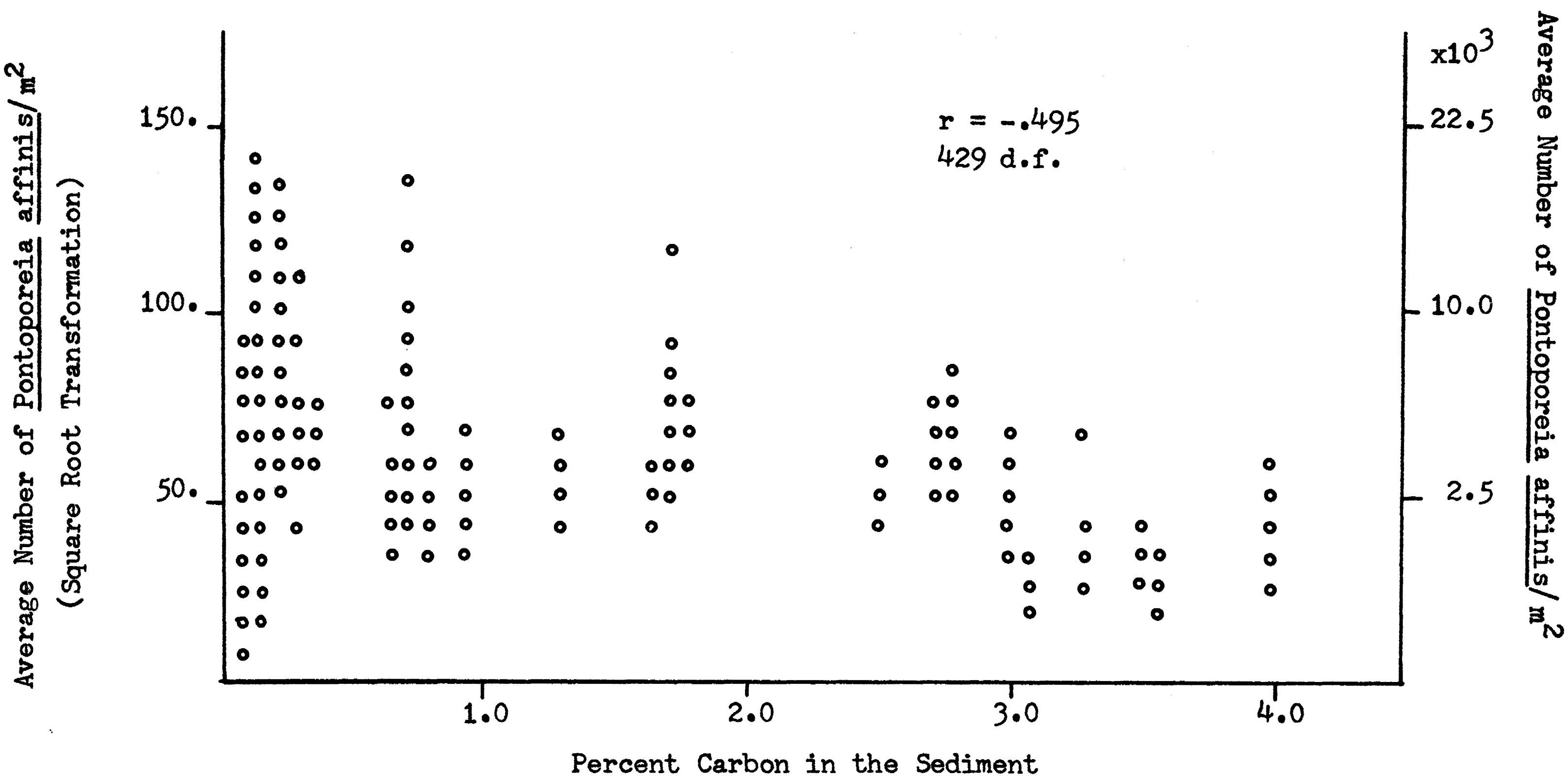


FIG. 40. Average number of Pontoporeia affinis per square meter obtained at each station visit versus percent organic carbon in the sediment.

the wide range of variability that exists in the average number of Pontoporeia found in the sediments containing little organic carbon.

Distance from Shore: Samples of Pontoporeia were combined into groups that were the same distance from shore (Fig. 41). Stations two miles from shore represented the most inshore sampling area while a station 38 miles from shore was the greatest sampling distance. There appears to be a general inverse relationship between amphipod abundance and distance from shore. The greatest variability in amphipod abundance occurred at the more inshore stations (Fig. 42).

Stepwise Multiple Regression Analysis of Environmental Parameters

The lake was first treated as a single system in the examination of the interrelationships of Pontoporeia and its environment. It was next divided into four depth zones: 10-35 m, 36-65 m, 66-105 m and greater than 105 m. Stations in the 10-35 m zone were considered the sublittoral and those deeper than 35 m, profundal.

First the simple correlation coefficients were calculated for the four depth zones and all depths combined, then the stepwise multiple regression equation was computed for these data. A 5 percent level of significance was chosen for the F test that controls the likelihood of committing the error of entering a variable into the prediction equation when it is insignificant. This same level of significance was also used for the F test that controls the error of removing a variable from the equation when it is significant. A multiple correlation coefficient and a

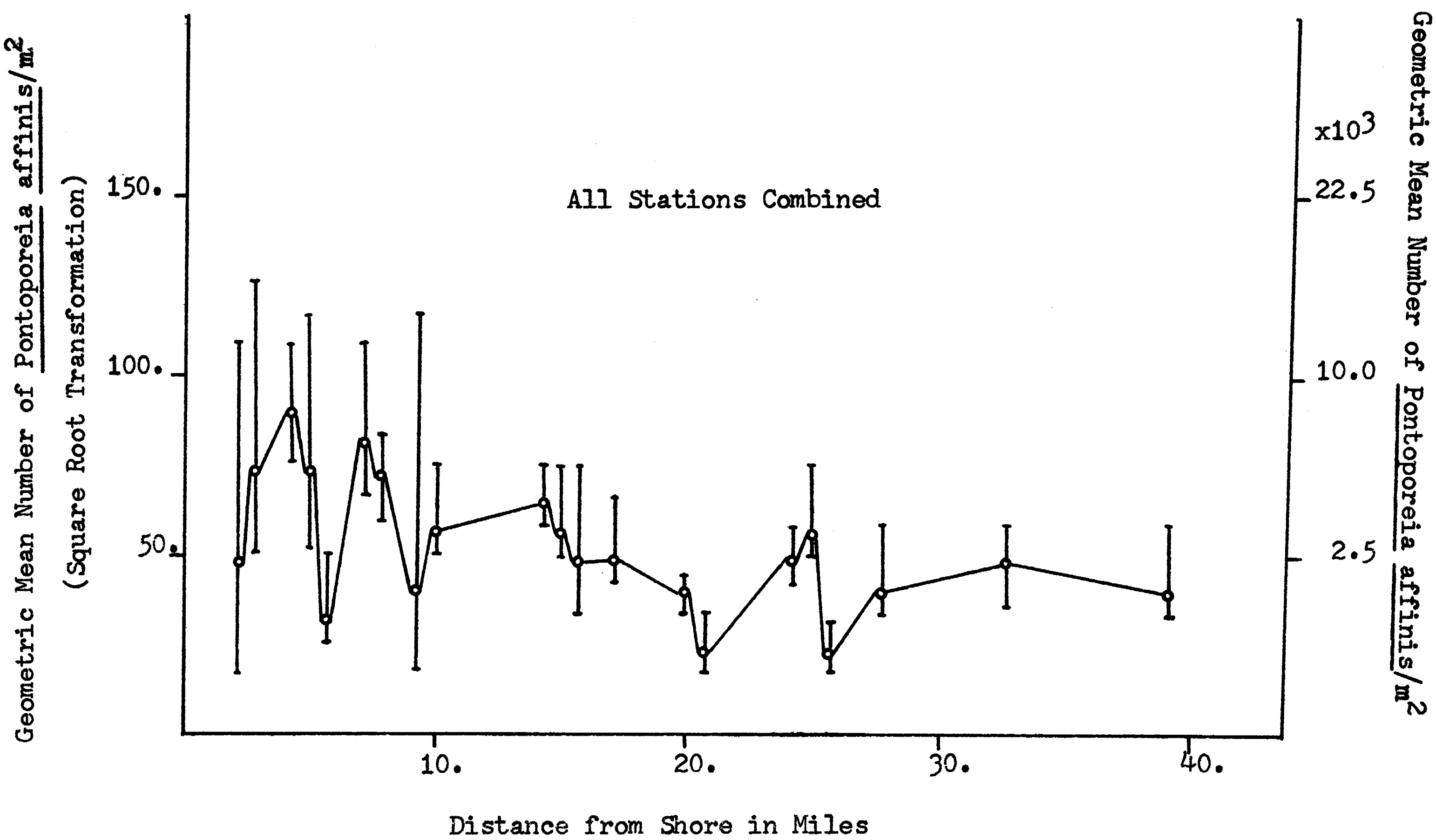


FIG. 41. Averagc number of Pontoporeia affinis per square meter pooled by intervals of one mile versus distance from shore.

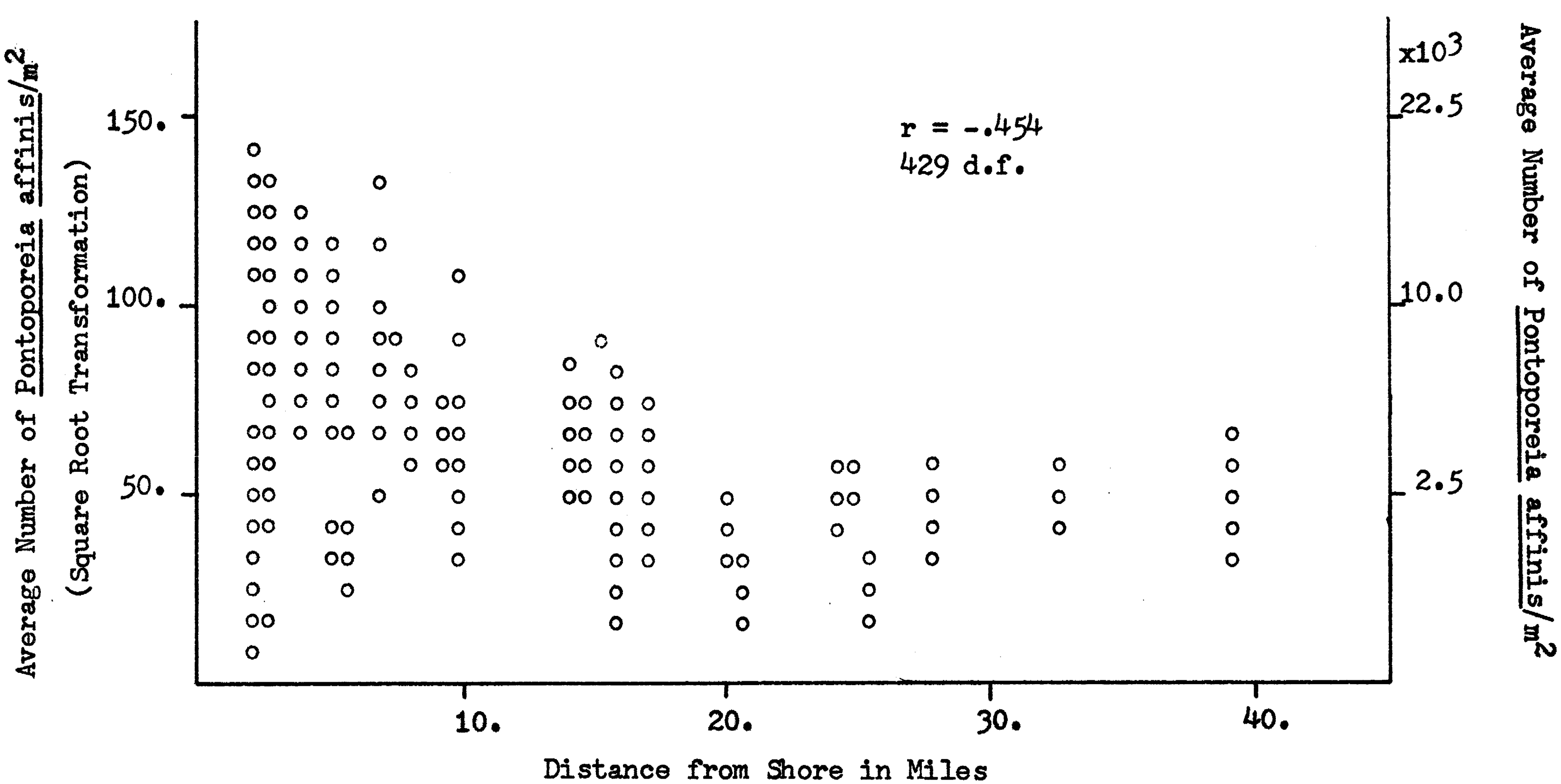


FIG. 42. Average number of Pontoporeia affinis per square meter obtained at each station visit versus distance from shore.

coefficient of determination, in addition to the multiple regression equation, were also calculated for the depth zones.

The multiple correlation coefficient measures the closeness with which the multiple regression equation fits the observed points, i.e. the multiple correlation coefficient measures the combined effect of the environmental parameters on the abundance of this amphipod. The coefficient of determination, the square of the multiple correlation coefficient, shows how much of the variability in the abundance of these organisms is explained by the environmental factors.

Table 4 shows the correlation coefficient of Pontoporeia and the environmental factors for the four depth zones and all depths combined. Day of year is significant only at the 10-35 m zone. Depth and depth squared show a significant positive relationship for the 10-35 m zone while the remaining depth zones show a significant negative relationship. When the lake is treated as a single system, there is a very significant negative relationship between depth and amphipod abundance.

There does not appear to be a significant relationship between amphipods and surface or bottom temperature for any of the four depth zones. However, if the lake is treated as a unit, there is a slightly significant positive relationship for both water temperatures.

There is no significant relationship in the sediment types, for 10-35 m, a slightly significant negative relationship from 36-105 m, a slightly positive relationship at depths greater than 105 m and a very

TABLE 4. The relationships that exist between _Pontoporeia affinis_ and the physical and biological environments of Lake Michigan as determined by correlation analysis.

		Depth Zones				All Depths Combined
	Variable	10-35 m	36-65 m	66-105 m	> 105 m	
X_1	Day of year	.214*	.119	-.119	-.119	-.027
X_2	Depth m	.557**	-.190	-.506**	-.769**	-.615**
X_3	Depth squared	.550**	-.195*	-.501**	-.763**	-.593**
X_4	Surface temperature	.056	.038	-.067	.016	.102**
X_5	Bottom temperature	-.010	.011	.014	.051	.277**
X_6	Sediment type	-.197	-.227*	-.258**	.288**	-.453**
X_7	Percent carbon in the sediments	.223*	-.051	.252*	-.543*	-.495**
X_8	Distance from shore	.303**	-.496**	-.295**	.007	-.454**
X_9	Oligochaeta	.335**	.289**	.431**	.605**	.599**
X_{10}	Sphaeriidae	.559**	.556**	.587**	.605**	.744**
X_{11}	Chironomidae	.276**	.226*	.290**	.396**	.443**
		92 d.f.	105 d.f.	92 d.f.	134 d.f.	429 d.f.

* Significant at 5%
** Significant at 1%

significant inverse relationship when all stations were combined.

Oligochaetes, sphaeriids, and chironomids showed a significant positive association with Pontoporeia for the four depth zones and when all depths were combined.

Tables 5 and 6 show the multiple regression equations for the four depth zones and all depths combined. These equations contain only the environmental factors that contributed a "significant" amount of information about changes in the abundance of Pontoporeia. In addition to the regression equation, a table was constructed to show the relative proportion that each significant variable contributes to the multiple correlation coefficient and the coefficient of determination.

Normally, when multiple regression is utilized in the analysis of biological systems, considerable "noise" is caused by the incomplete measurement of all possible variables or the inability to measure the variables with precision. This excessive noise results in a small multiple correlation coefficient. The large multiple correlation coefficients of Tables 5 and 6 indicated that the physical and biological factors used in this study contributed considerable information about changes in Pontoporeia abundance.

Table 5 shows that the abundance of sphaeriids statistically contributed the most in explaining the fluctuation of amphipod density at the 10-35 m zone. The other significant parameters, in their order of importance, were depth, depth squared, surface temperature, sediment

TABLE 5. The proportion of the multiple correlation coefficient (R) and the coefficient of determination, expressed as a percentage, (R^2) that each statistically significant variable contributes to the multiple regression equation of the four depth zones in Lake Michigan. The dependent variable of the multiple regression equation (Y) is represented by the numbers of Pontoporeia affinis/m^2.

	Variable	R	R^2
	10-35 m		
X_{10}	Sphaeriidae	.559	31.3
X_2	Depth	.084	10.1
X_3	Depth squared	.039	5.1
X_4	Surface temperature	.031	4.5
X_6	Sediment type	.028	3.9
X_8	Distance from shore	.015	2.2
		.756	57.1
	$Y = .756 + 7.927X_2 - .122X_3 + 1.485X_4 - 7.106X_6 - 4.074X_8 + 3.431X_{10}$		
	36-65 m		
X_{10}	Sphaeriidae	.556	30.9
X_6	Sediment type	.043	5.0
		.599	35.9
	$Y = 48.104 - 3.804X_6 + 2.757X_{10}$		
	66-105 m		
X_{10}	Sphaeriidae	.586	34.4
X_3	Depth squared	.033	5.2
X_{11}	Chironomidae	.034	3.0
X_9	Oligochaeta	.024	3.6
		.677	45.6
	$Y = 39.592 - .009X_3 + 1.032X_9 + 1.766X_{10} + .926X_{11}$		
	≥ 105 m		
X_2	Depth	.769	59.1
X_9	Oliogochaeta	.037	5.9
X_{10}	Sphaeriidae	.020	3.3
		.826	68.3
	$Y = 49.216 - .133X_2 + 1.371X_9 + 1.732X_{10}$		

TABLE 6. The proportion of the multiple correlation coefficient (R) and the coefficient of determination, expressed as a percentage, (R^2) that each statistically significant variable contributes to the multiple regression equation of all depths combined in Lake Michigan. The dependent variable of the multiple regression equation (Y) is represented by the numbers of Pontoporeia affinis/m^2.

	Variable	R	R^2
X_{10}	Sphaeriidae	.744	53.3
X_3	Depth squared	.018	2.8
X_{11}	Chironomidae	.008	1.2
X_2	Depth	.007	1.2
X_7	Distance from shore	.007	1.0
X_1	Day of year	.005	.7
X_6	Sediment type	.005	.8
X_5	Bottom temperature	.002	.4
		.796	63.4

$$Y = 12.333 + .049X_1 + .360X_2 - 12.174X_3 + .779X_5 - 4.193X_6 - 3.476X_7 + 2.874X_{10} + 2.355X_{11}$$

type, and distance from shore. Approximately 57 percent of the variablilty in amphipod abundance was attributable to these six variables.

Only two parameters, sphaeriids and sediment type, were statistically significant in explaining the deviations in amphipod density of the 36-65 m depth zone. The sphaeriids accounted for 31 percent of the changes in Pontoporeia abundance while the sediment type contributed only 5 percent.

Within the 66-105 m depth zone the abundance of sphaeriids statistically represented the most important parameter, followed by depth

squared, chironomids, and oligochaetes in that order of importance. These four variables accounted for approximately 46 percent of the fluctuation of Pontoporeia abundance.

At depths greater than 105 m, depth became the most important factor in determining the variability in amphipod abundance followed by ologochaetes and sphaeriids, in that order. These three parameters accounted for 68 percent of the fluctuations in amphipod density.

When the lake was treated as a single unit, additional parameters became important in determining the fluctuations of Pontoporeia density. The sphaeriids were the most important, followed by depth squared, chironomids, depth, distance from shore, day of the year, sediment type, and bottom temperature. These eight variables accounted for approximately 63 percent of the changes in the amphipod counts. However, the last seven of these eight parameters contributed only eight percent of the coefficient of determination.

When the lake was subdivided into four depth zones, three environmental parameters, day of year, percent carbon in the sediment, and bottom temperature had no influencing effects on the amphipod populations. When the lake was treated as a single system, surface temperature, percent carbon in the sediments and oligochaetes did not significantly affect amphipod abundance. Multiple regression analysis indicated that the density of these organisms is not influenced by the percent carbon in the sediment.

It appeared that turbulence caused by waves might contribute information about changes of Pontoporeia abundance in the lake. Information collected at the stations of the C, D, and E transects and wave heights measured by the personnel of the three car ferries were utilized in the subsequent statistical analysis. Wave heights were coded from 0 to 5 with a rank of one representing a wave one meter high, a rank of two a wave two meters high, and so forth. The largest wave height noted for a period three days prior to and including the sampling day was recorded for the stations of each transect. The lake was treated as a single system and then divided into two depth zones: 20-50 m and less than 105 m. The shallowest station of the three transects was 20 m.

Table 7 shows the simple correlation coefficients of amphipod abundance versus the environmental and biological parameters. There does not appear to be any significant relationship between Pontoporeia and wave height for the 20-50 m zone, less that 105 m, and all depths combined. The multiple regression equations for these data also indicated that wave height is not associated with Pontoporeia abundance. Unfortunately, the turbulence caused by waves would achieve its grestest effects at depths less than 20 m, which would indicate that these results are inconclusive.

SEASONAL DISTRIBUTION

In the investigation of the seasonal abundance patterns of Pontoporeia, the fundamental question concerning the reliability of data collected at

TABLE 7. The relationships that exist between Pontoporeia affinis and the physical and biological environment as determined by correlation analysis for the stations of the C, D, and E transects.

	Variable	20-50 m	< 105 m	All Depths
X_1	Wave height	.038	.019	.017
X_2	Day of year	.167	.023	-.021
X_3	Depth	-.125	-.617**	-.823**
X_4	Depth squared	-.146	-.614**	-.748**
X_5	Surface temperature	.134	.013	.080
X_6	Bottom temperature	.181	.342**	.476**
X_7	Sediment type	.049	-.483**	-.610**
X_8	Percent carbon in sediment	-.087	-.336**	-.673**
X_9	Distance from shore	-.146	-.622**	-.618**
X_{10}	Oligochaeta	.258*	.472**	.701**
X_{11}	Sphaeriidae	.320**	.630**	.829**
X_{12}	Chironomidae	.333**	.373**	.586**
	* Significant at 5% ** Significant at 1%	70 d.f.	136 d.f.	267 d.f.

sequential time intervals was examined by sampling the stations of the C transect on two successive days, 9 and 10 August 1966 (Fig. 43). It was felt that the density of Pontoporeia at these stations should not radically change within a 24 hour period, and any significant deviation in amphipod density between the two collecting dates would be the result of experi-

mental error or inefficient sampling techniques. The Wilcoxon sign rank test indicated there was no significant difference in the abundance of amphipods between the stations of the two sampling dates.

The result of the rank test justified the combining of the two data sets for each station to obtain an estimate of sample variation. The coefficient of variation, which measures the relative variation of amphipod abundance, was calculated for these combined data (Fig. 43). There is no particular pattern to the relative variation with respect to depth or position along the transect. The average relative variation for the seven combined stations was 9.3 percent.

The amphipod counts for all 35 stations of the long-term study area were pooled for each month of the three sampling seasons (Fig. 44). A Kruskal-Wallis sign rank test indicated there was no significant difference between the average standing crop of the three sampling seasons. Table 8 shows the grand geometric mean number of amphipods of all depths combined for each of the sampling seasons and the results of the Kruskal-Wallis test. The average number of amphipods for 1964 is 53 while the means for 1965 and 1966 are 55 and 54 respectively.

The Pontoporeia collected at the 35 stations were also combined into four depth zones: 10-35 m, 36-65 m, 66-105 m, and greater than 105 m for the monthly sampling periods (Fig. 44). A Kruskal-Wallis test was calculated to determine if the average density of amphipods was significantly different for the four depth zones. A significant differ-

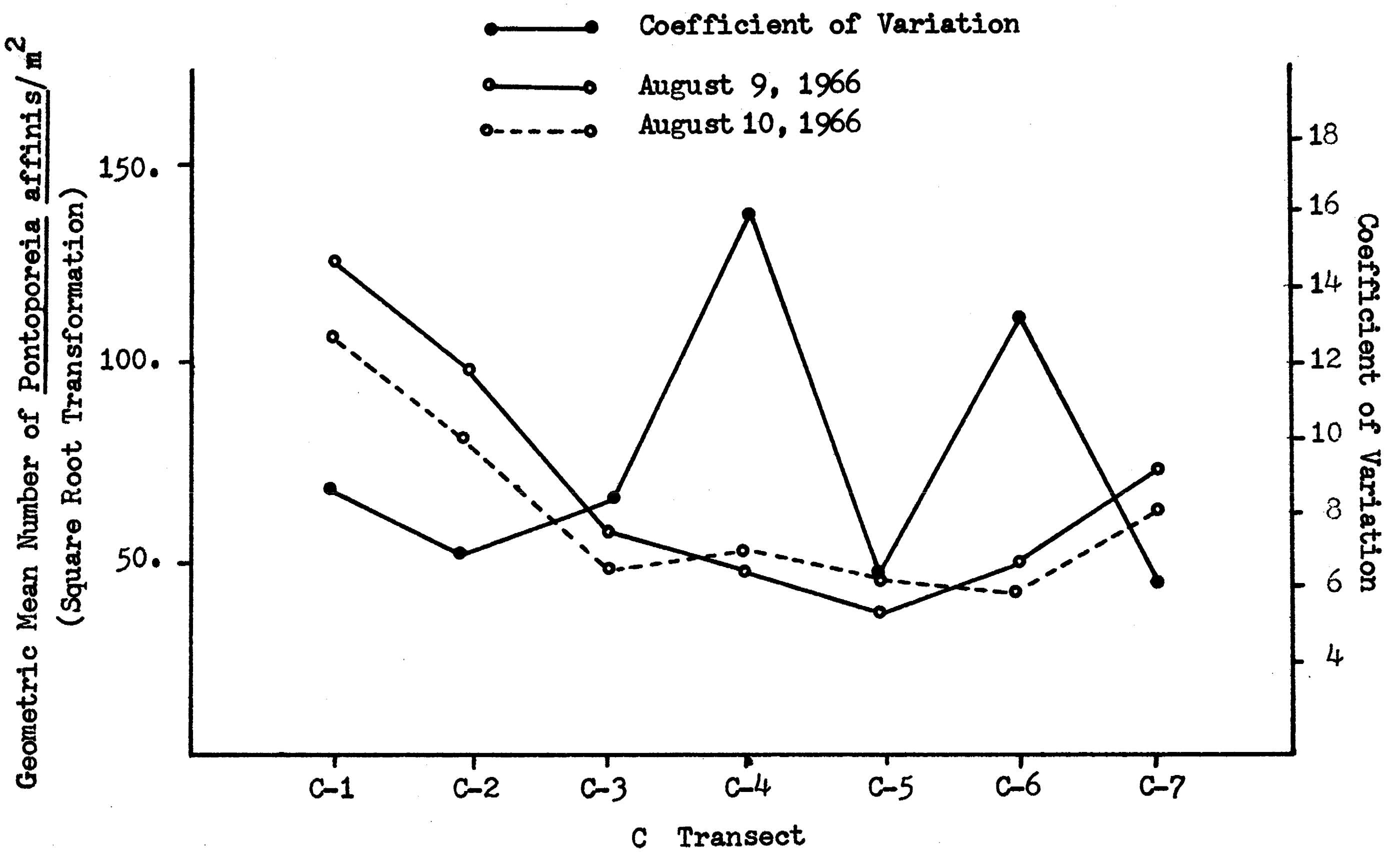


FIG. 43. A comparison of the Pontoporeia affinis density of the seven stations located on the C transect, sampled 9 and 10 August 1966, and the coefficient of variation for the combined sampling dates.

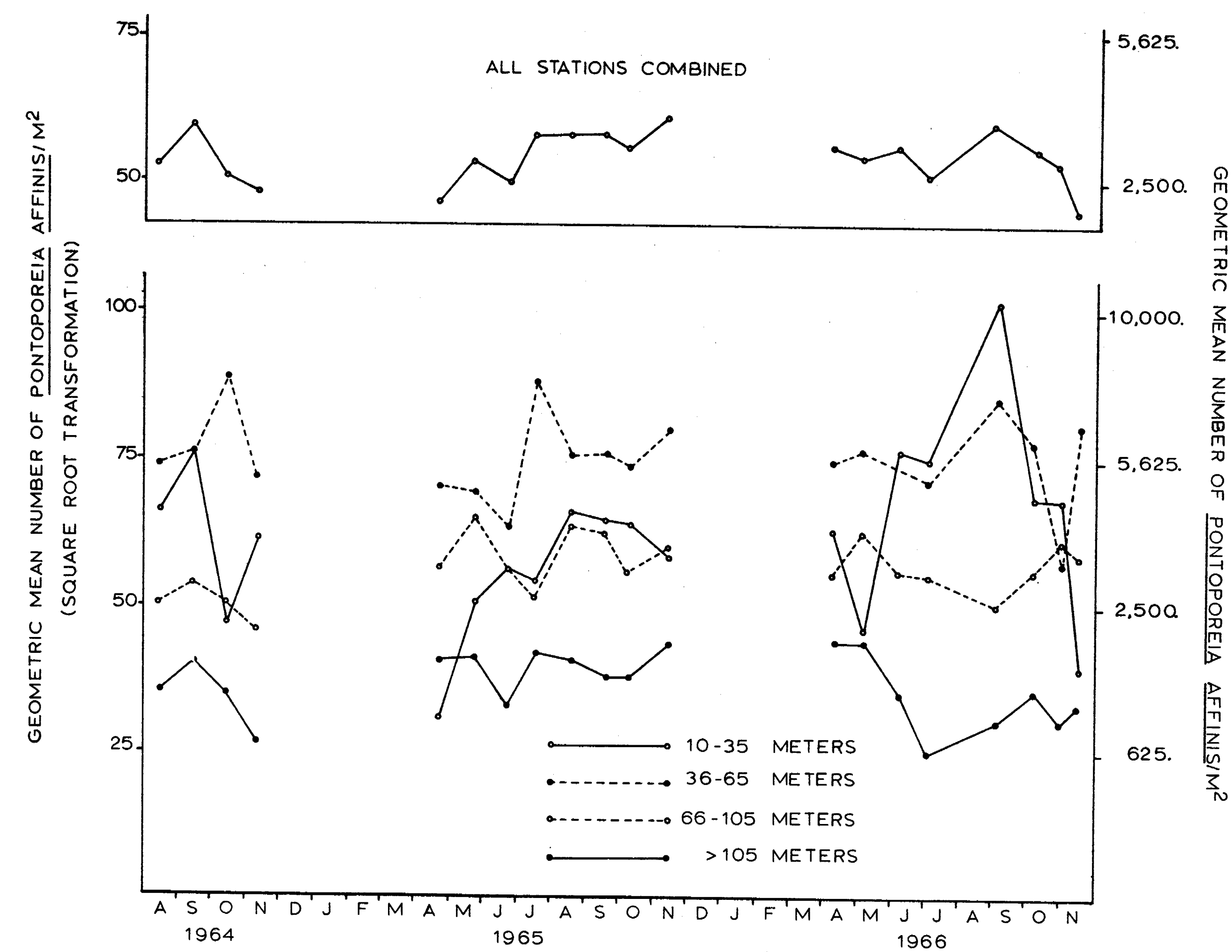


FIG. 44. Patterns of seasonal abundance of Pontoporeia affinis for the four depth zones and all depths combined.

ence in abundance was found among the four depth zones; the density of numbers was greatest in the 36-65 m zone followed, in order of decreasing abundance, by the 10-35 m, 65-105 m, and greater than 105 m zone.

Pooled amphipod counts of the four depth zones were again treated with the Kruskal-Wallis rank test to determine if the standing crop of amphipods were significantly different for the three sampling periods. This test showed no apparent difference in the standing crop for the 10-35 m, 36-65 m, and greater than 105 m depth zones. The grand geometric mean number of Pontoporeia for the four depth zones of the three sampling seasons and the results of the Kruskal-Wallis test are presented in Table 8.

A reexamination of Figure 44 and Table 8 shows that although there was no significant seasonal variation in the abundance of amphipods at the 10-35 m zone there was considerable variation within comparable sampling periods. In 1965 there was a general increase in the popula-

TABLE 8. The grand geometric mean number of Pontoporeia affinis for the three sampling seasons. H represents the results of the Kruskal-Wallis test.

Depth Zones	1964	1965	1966	H
10-35 m	62	55	67	2.78
36-65 m	78	75	75	.52
66-105 m	50	59	58	7.76*
>105 m	35	40	36	3.81
All stations combined	53	55	54	.55

* Significant at 5%

tion from April to August followed by a slight decline from August to November. The 1966 population decreased in numbers from March to April, increased from April to August, and then decreased sharply from August to November.

A Spearman rank correlation coefficient was computed for the four depth zones and for all depths combined to determine if any association patterns of Pontoporeia abundance existed among the three sampling seasons (Table 9). The results indicated no correlation in the seasonal patterns of abundance for any of the four depth zones. Only the 10-35 and 36-65 m zones showed any association when all the stations were combined.

Figure 45 shows the patterns of seasonal abundance of Pontoporeia for the seven stations of the C transect. The Kruskal-Wallis test indicated that only at station C-3 was the average standing crop significantly different for the three sampling seasons; there appeared to be no seasonal differences at the other C stations. The grand mean number of amphipods for these 7 stations for the three sampling seasons and the results of the Kruskal-Wallis test are presented in Table 10.

Figure 45 indicates that the patterns of amphipod abundance for 1965 and 1966 are quite similar for stations C-2, C-3, C-6, and C-7, and changes in amphipod counts of stations C-4 and C-5 were similar in many respects. The seasonal changes at station C-1, however, differ strongly from the other six stations.

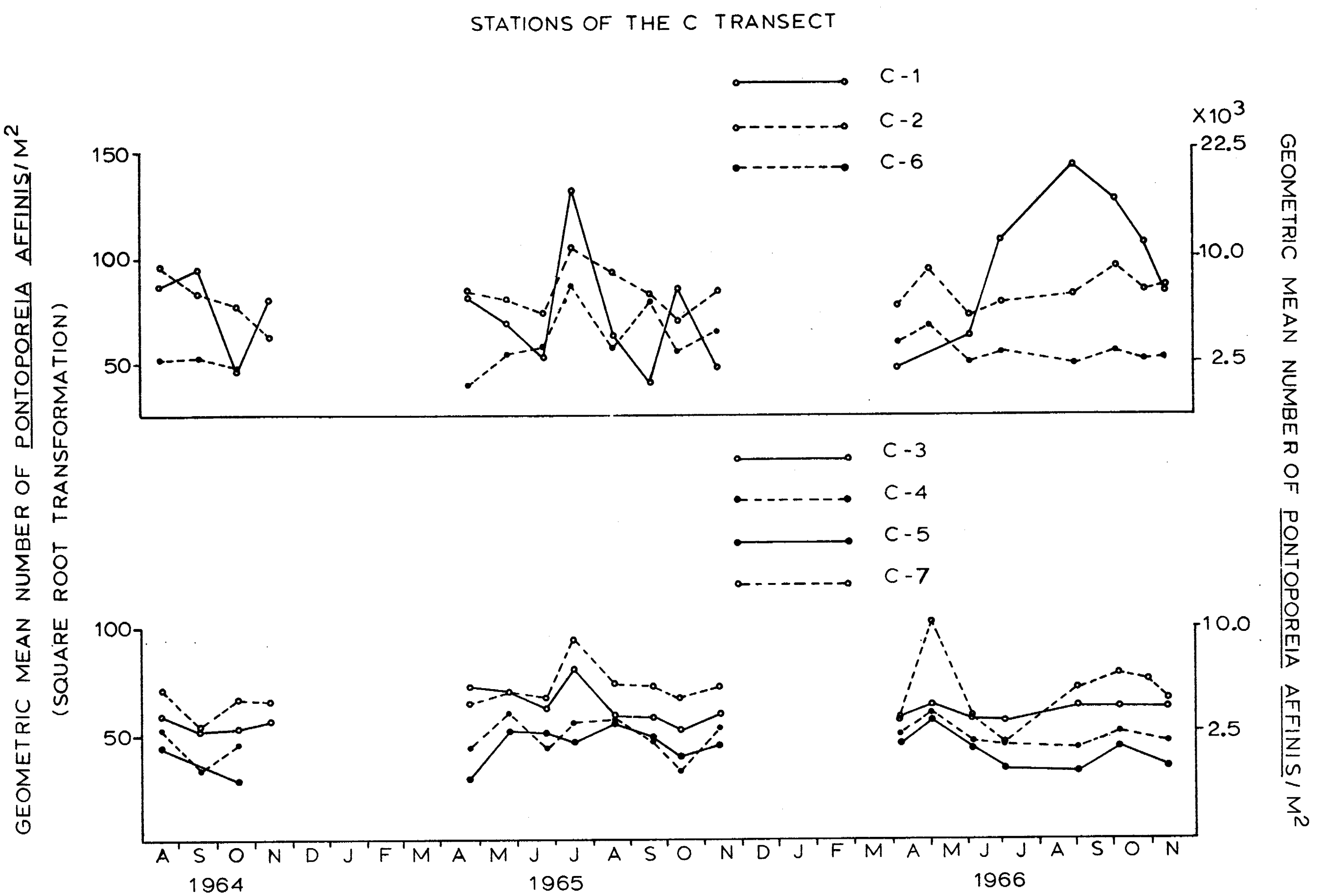


FIG. 45. Patterns of seasonal abundance of Pontoporeia affinis for the seven stations of the C transect.

A Spearman rank correlation test was calculated for stations C-2 through C-7 in order to determine if there was a significant association in the patterns of Pontoporeia abundance (Table 11). The results show that these stations have similar patterns of seasonal variation, particularly when adjacent stations are considered.

The seasonal patterns of amphipod abundance for the seven stations of the C transect were next compared with the abundance patterns of their respective depth zones by the Spearman rank correlation (Table 12). Although only stations C-2 and C-4 showed any significant association with their respective depth zones, all the correlation coefficients were positive, which would indicate that, in general, the seasonal fluctuations of Pontoporeia of the seven C stations were similar to the fluctuations of their respective depth zones.

TABLE 9. Spearman rank correlation coefficients indicating the degree of association that occurred among the patterns of seasonal abundance of Pontoporeia affinis for the four depth zones and all depths combined.

	10-35 m	36-65 m	66-105 m	>105 m
36-65 m	-.085			
66-105 m	-.204	-.188		
>105 m	-.400	.421	.429	
All stations combined	.529	.459*	.119	.415

* Significant at 5%

TABLE 10. The grand geometric mean number of Pontoporeia affinis for the three sampling seasons of the seven stations of the C transect. H represents the results of the Kruskal-Wallis test.

Station	Average Depth m	1964	1965	1966	H
C-1	20	77	72	99	3.20
C-2	50	80	85	84	.12
C-3	77	56	67	63	13.47**
C-4	108	46	51	49	.62
C-5	157	39	47	43	1.95
C-6	99	49	58	49	2.63
C-7	55	65	72	70	.73

** Significant at 1%

TABLE 11. Spearman rank correlation coefficients indicating the degree of association that occurred among the patterns of seasonal abundance of Pontoporeia affinis for stations C-2 thru C-7 for the three sampling seasons.

	C-2	C-3	C-4	C-5	C-6
C-3	.648**				
C-4	.566*	.578*			
C-5	.258	.297	.737**		
C-6	.637**	.350	.765**	.721**	
C-7	.783**	.594*	.658**	.495	.709**

* Significant at 5%
** Significant at 1%

TABLE 12. Spearman rank correlation coefficients indicating the degree of association that occurred between the patterns of seasonal abundance of Pontoporeia affinis for the stations of the C transect and then respective depth zones.

C-1	versus	10-35m	.422
C-2	versus	36-65m	.467*
C-3	versus	65-105m	.405
C-4	versus	> 105m	.515*
C-5	versus	> 105m	.432
C-6	versus	66-105m	.175
C-7	versus	36-65m	.266

* Significant at 5%

PATTERNS OF SPATIAL ABUNDANCE

All observations from each station of the five cross-lake transects were pooled for the three sampling periods to provide information on the spatial standing crop of Pontoporeia (Fig. 46). These results indicated that its abundance at shallow inshore stations A-1 and A-6 was lower than at other stations on the A transect, which were located at greater depths and farther from shore. The remaining four transects show a general tendency for average amphipod counts at the stations located in the deeper portions of the lake to be less than the shallower inshore stations. The standard deviations of amphipod density of the inshore stations are generally greater than those of the deeper stations. Stations

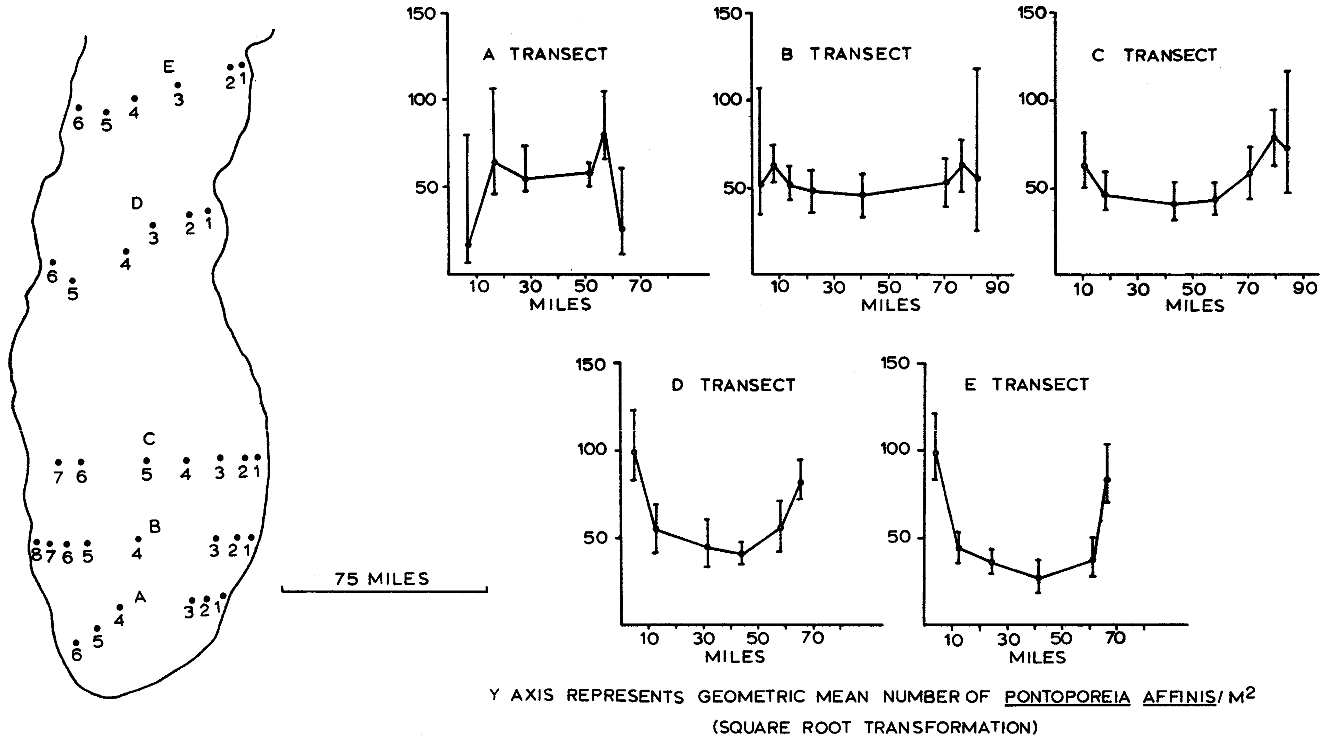


FIG. 46. The average density of Pontoporeia affinis for the stations of the five transects. The distance from shore is measured from the west side of the lake.

situated in the northern basin of the lake have, in general, more amphipods/m^2 than stations located in the southern basin that are situated at comparable depths.

It is difficult to compare directly the amphipod counts at the 35 stations because they were located at different depths and it has been shown that depth strongly influences the abundance of P. affinis in an inverse manner. In order to make direct comparison possible, the effect of depth on amphipod density was removed by first calculating the density-depth regression equation $Y = 81.04 - 0.232X$ where Y represents the average number of amphipods per station stop, X the depth per station stop, 81.04 the intercept, and -0.232 the regression coefficient. A second order polynomial relationship for depth was important in explaining fluctuations in amphipod abundance when all environmental parameters were considered. However, when the relationship between amphipod density and depth was considered independently of the other environmental factors, the squared term for depth was not significant.

The grand average density of amphipods and the average depth must fall on the regression line. In removing the effect of depth, the deviations of Y about the regression line were shifted so these deviations occurred about a regression line that had a slope of zero and an intercept equal to the grand average density of amphipods. This was accomplished by modifying the above regression equation in the following fashion: $Y = y + 0.232(X-85.9)$ where y was the observed average value

of amphipods per station stop, X the depth of the station stop, 0.232 the regression slope, 85.9 the average depth, and Y the estimated density of amphipod with the effect of depth removed.

Figure 47 shows that the pooled average density of Pontoporeia at stations A-1 and A-6 is much lower than the remaining stations of the A transect after the effect of depth was removed. The average abundance of amphipods found at shallow station B-8 also appears to be lower than the remaining stations of the B transect. The density of amphipods at station C-2 appears to be somewhat higher than the other stations of the C transect, and the density at stations D-6 and E-6 also appears to be higher than the other stations on their respective transects.

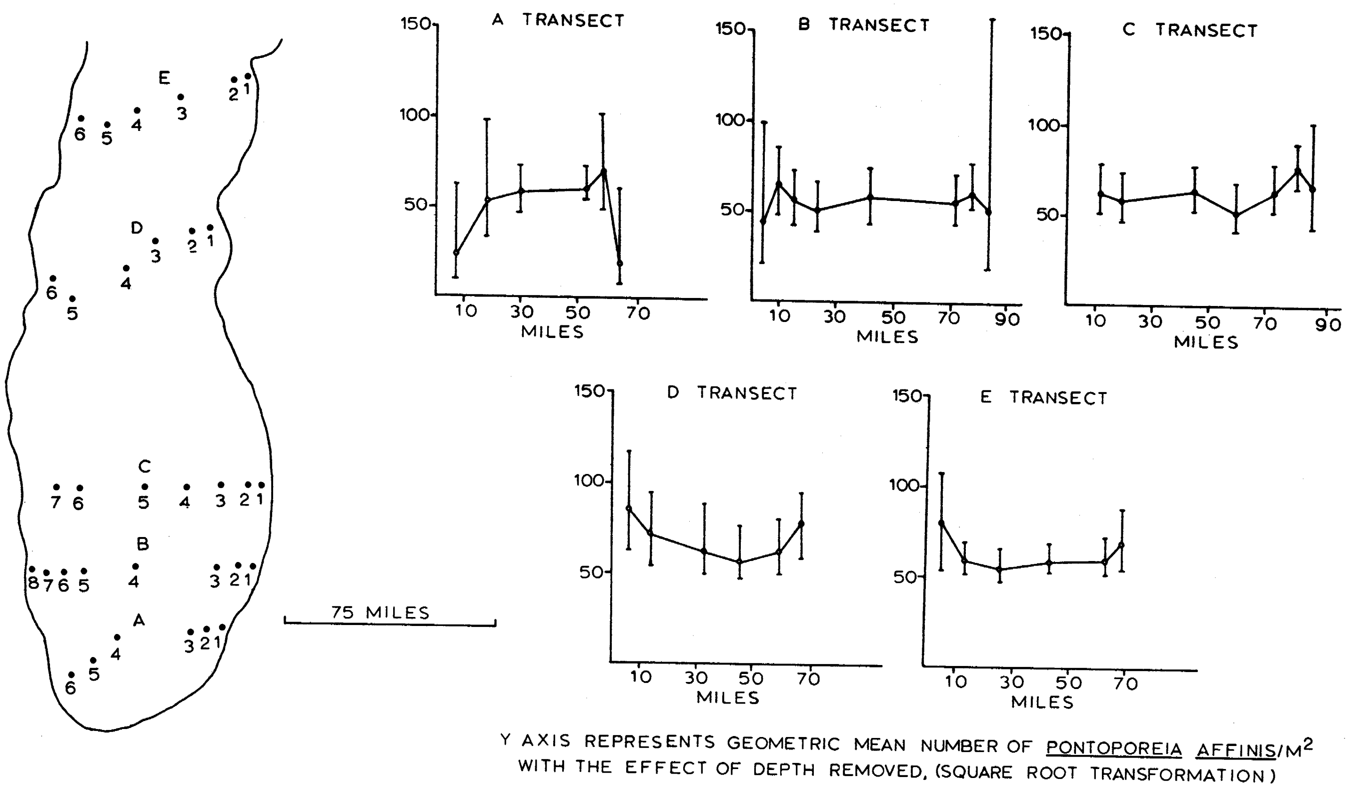


FIG. 47. The average density of Pontoporeia affinis for the stations of the five transects with the effect of depth removed. The distance from shore is measured from the west side of the lake.

DISCUSSION

REPRODUCTION

The results of the present investigation indicate that at least three distinct breeding populations of Pontoporeia occur in Lake Michigan. The data strongly suggest that amphipods living at a depth of about 10m mature in one year, while those in approximately the 20-35m zone require two years to mature. The reproductive season seems to be completed by late May-early June for these populations. Amphipods living at depths greater than 35m may require at least three years to mature, and the population there breeds intermittently throughout the spring, summer, and fall. Insufficient data were obtained to determine whether breeding also takes place in winter.

Juday and Birge (1927) found that the breeding season of Pontoporeia extended from December to May in Green Lake, Wis., and there the population required two years to mature. Bousfield (1958) reported ovigerous females from November to April in Canadian oligotrophic lakes, and indicated that the life span was slightly more than two years. Larkin (1948) found that this amphipod had a life span of 2 and perhaps 3 years in Great Slave Lake. Teter (1960) felt that P. affinis matured in one year in Lake Huron while Cooper (1962) found a one year life cycle at a depth of 12 m and a two year life cycle at a depth of 35 m in

South Bay, Lake Huron. Green (1965) found a maturation period of 2 years in Cayuga Lake, New York, and Segerstråle (1950) reported that *P. affinis* matured in one year at a depth of 3 m and required 3 years to mature at a depth of 35 m in the Baltic Sea. Summer breeding, which appears to be common in North American oligotrophic lakes, was first recorded in the Baltic Sea in 1967 by Segerstråle and represents the only record of summer breeding in Eurasia.

Observed variations in the duration of the breeding season and development are likely attributable to corresponding variations in water temperature. In Lake Michigan, the average bottom temperature of the 10-15 m depth zone, from March to October, is approximately 9°C. The average bottom temperature at 20-35 and 36-86 m depth zones for the same time interval is approximately 7°C and 5°C respectively. Depths beyond 86 m have an average bottom temperature that is slightly less than 4°C from March to October. An examination of bottom temperature records of the present study indicated that *Pontoporeia* did not breed at any depth when the bottom temperature exceeded 7°C. Samter and Weltner (1904) observed that temperatures greater than 7°C prevented egg production and concluded that the type and locality of a lake determined to a large extent the time and duration of the reproductive period.

PATTERNS OF SPATIAL DISTRIBUTION

Short-Term Study Area

Living organisms are subject to a multitude of variable factors,

both intrinsic and extrinsic, that affect their behavior, performance, and survival. The effects of these influencing factors are not independent but exhibit numerous complex interactions of which we know little. Within any defined geographical area, some factors will remain constant for a short time while others may vary. In general, the smaller the area the greater will be the number of constant factors. In the short-term investigation a small study area was sampled rapidly in order to hold constant as many environmental factors as possible.

Populations are either randomly or nonrandomly distributed depending on the effects of the environmental factors. There are two categories of departure from randomness: a contagious distribution where the individuals of the population tend to be aggregated, and a regular dispersal where the individuals of the population tend to be uniformly space. It is generally observed that practically all biological populations are contagiously dispersed and that few populations are randomly spaced.

Several theoretical distributions have been proposed to explain these dispersal patterns and apparently some of these conform to empirical data. In the short-term study area two such theoretical distributions were considered, the normal and the Poisson. If members of a population conform to a Poisson distribution then the density of individuals is low relative to the possible density that cound exist in that area, and the members of the population are considered to be randomly spaced. If the effects of all environmental factors are small or the environmental fac-

tors are randomly distributed, the individuals will be dispersed as a normal distribution. This distribution can also be considered the result of one or more organisms within a sample unit influencing the probability of other organisms occurring in the same sample.

In this investigation of the distributional patterns it was necessary to examine the number of individuals in several quadrats of constant size. However, there is a major disadvantage in quadrat analysis in that changes in frequency distribution occur when the quadrat size is altered. When the quadrat size is increased it is more likely to contain many individuals and less likely to contain no individuals. Preston (1948) has indicated that in order for the Poisson distribution to be valid the quadrat must contain more space than is actually utilized by the organisms. As the quadrat size is increased, the environmental factors become more variable and it becomes more difficult to discriminate between patterns of microdispersion, i.e. within a large quadrat highly populated areas are pooled with sparsely populated areas. The sampling area of the hand coring device in the short-term study area contained more space than was utilized by the macrobenthic invertebrates but was sufficiently small to measure adequately the microdistribution of the organisms.

Replicated random sampling was selected as one method of data collection because it not only obtains an estimate of the mean but also an estimate of the variability of the mean. Because the mean is independent of the variance in the normal distribution and equal to the variance

in the Poisson distribution, the variance-mean regression is a useful tool in determining the distributional patterns. It is apparent from the short-term study area that small and total Pontoporeia conformed to the normal distribution while large Pontoporeia fitted the Poisson distribution. In spite of the existance of only 15 bivariate observations and 13 degrees of freedom, the trends of these variance-mean regressions strongly indicated these two distributional patterns.

Systematic sampling was chosen as the other method of data collection because it provided an easier method of obtaining underwater samples. However, systematic sampling has two potential disadvantages. If the populations or environmental factors contain a periodic variation, and if intervals between successive systematic samples happen to correspond with this variation, the resulting mean may be seriously biased. Further, with systematic sampling there is no reliable method of estimating the standard error of the sampling mean.

Six intersecting transects were used to provide information about the linear distribution of the organisms and to sample extensively the inner region of the sampling area. It appeared that none of the amphipod categories showed any interaction between adjacent sampling sites. Thus, each sample appeared to be independent of the others.

Since 45 samples were randomly chosen and the 43 systematic samples appeared to be independent of each other, they were pooled in

constructing the frequency histograms. The chi square test for goodness of fit comparing the theoretical distributions with the observed frequency histograms showed that small and total Pontoporeia followed the normal distribution while large Pontoporeia conformed to the Poisson.

Henson (1954) showed in a study of Cayuga Lake that Pontoporeia larger than 6 mm in length were randomly distributed, those 4 to 5 mm in length were distributed on the "borderline" between randomness and contagiousness, and those smaller than 3 mm in length were contagiously distributed. Green (1965), also in an investigation of Cayuga Lake, found that adult Pontoporeia were randomly distirubted while the 1-2 mm size group were strongly clumped.

The investigations of Henson and Green and the present study all indicate that larger Pontoporeia are randomly distributed within the sediments. It was difficult to compare the distributional patterns of the smaller amphipods from the three studies because Henson utilized two small-size categories. Both Henson and Green used the variance-mean relationship to determine if the size groups were rendomly distributed. The smallest size group of the short-term investigation of the present work was tested in the same manner and also found to be contagiously distributed.

Long-Term Study Area

Sampling variability (heterogeneity of error) may be classified as irregular and regular. Irregular error is characterized by certain

samples possessing considerably more variability than others with no apparent relation between means and variances. Regular heterogeneity usually arises from some type of nonnormality in the data with the variability of the samples being related to the sample means (Steel and Torrie 1960).

It is often difficult to interpret the causes of variance-mean interaction but the variance of either the Poisson or binomial distribution is functionally related to the mean. Evans (1952) pointed out that if density is defined as the number of individuals per quadrat, density becomes directly proportional to quadrat size with a doubling in value occurring for each two-fold increase of quadrat area. The larger the quadrat the more likely it will contain many individuals and less likely to contain fewer individuals. A population sampled with one quadrat size may have its members distributed at random, yet the same individuals may be considered highly aggregated when another quadrat size is used. The *Pontoporeia* sampled in the long-term study area were converted to individuals/m^2 because the two samplers used had different grab areas. If samples are multiplied by a constant, the mean of these samples is increased by the multiple of the constant while the variance is increased by the square of the constant, which can affect the variance-mean relationship. It was indicated earlier that different size groups of *Pontoporeia* were either contagiously or randomly distributed. The relative proportion of these size groups will affect the distributional patterns.

The usual purpose of a transformation is to change the scale of measurements in order to make statistical analysis more valid. If the variance tends to change with the mean of the measurements, the variance will only be stabilized by a suitable change in the scale of the measurements. The transformed scale should be one for which real effects are linear and additive with the variation being normally distributed. Bartlett (1947) pointed out that when data consist of an integer type (whole numbers) with heterogeneity, especially if the data have been collected under field conditions, the square root transformation may be an appropriate transformation.

INTERSPECIFIC AND INTRASPECIFIC ASSOCIATIONS

The use of correlation coefficients as an index of biological association was questioned by Cole (1946) because the frequency distribution of organisms in samples commonly differ so widely from a random distribution that the validity of applying ordinary correlation methods to such data becomes highly questionable. Alley and Anderson (1968) showed that the Sphaeriidae and Chironomidae were randomly distributed while the Oligochaeta were distributed as a negative binomial distribution in the short-term study area. Thus, biological associations derived from correlation coefficients between large Pontoporeia, sphaeriids, and chironomids would not violate the objections of nonrandomness. In this investigation there was only concern for a significant positive or negative association, and not the degree of association, so it is felt that these

relationships are attributable to either biological or environmental phenomena.

It is often difficult to interpret the implications of biological association because the term itself is a loose definition which makes no distinction between relationships derived from mutualism, parasitism, symbiosis, and predation with those based on similar or dissimilar habitat requirements. The patterns of association are also influenced by the size of the units from which the samples are obtained. The relationships between organisms may vary from time to time.

Segerstråle (1965), in an investigation of the Baltic Sea, found an inverse relationship between the successful recruitment of the bivalve Macoma baltica and the abundance of Pontoporeia affinis. He also found a significant negative relationship between the abundance of the priapulid worm Halicryptus spinulosus and P. affinis. Segerstråle concluded that Pontoporeia ingested the spat of Macoma and the eggs of Halicryptus as it fed on detrital material. Although in Lake Michigan the larvae of the Sphaeriidae develop within the mantle cavity of the adult clam, the immature individuals, when released from the marsupia, are often small enough to be ingested by large amphipods. Because little is known about the complete feeding habits of Pontoporeia it is difficult to determine if this amphipod actively seeks small clams and the eggs of the oligochaetes.

The positive associations between total Pontoporeia and the other macrobenthic groups of the long-term study area probably reflect the

differences attributable to a larger quadrat sampling area and the greater variability between the 35 stations. It is felt that these results merely reflect the fact that, in general, a fairly large quadrat will mask patterns of microassociations and those regions within the lake that are preferred by Pontoporeia are also selected by the other macrobenthic groups.

ENVIRONMENTAL RELATIONSHIPS

Environmental Parameters Treated Individually

Depth: Eggleton (1937), in a study of the Lake Michigan macrobenthos, also found a concentration of Pontoporeia at the 30-40 m depth zone. The density increased from 10 to 30 m, and beyond 40 m the density sharply decreased. Merna (1960), also in an investigation of the Lake Michigan macrobenthos, did not find the 30 m concentration zone of Pontoporeia, however, his shallowest sampling depth was approximately 20 m. Marzolf (1963) found no correlation with depth in a study of Grand Traverse Bay, but his sampling depths began at 20 m.

Bottom Temperature: Gordeev (1952) reported that the optimum temperature range for Pontoporeia, as determined through laboratory studies, is 8.0 to 12.0°C. The upper limit of tolerance according to field observations is 14.0 to 20.0°C as reported by Samter and Weltner 1904; Ekman 1915; Thienemann 1928; Segerstråle 1937; and Bousfield 1958. It is evident from the present Lake Michigan field observations that this amphipod can tolerate an extreme range of bottom temperatures

and does not show any specific temperature preference.

Substrate Relationship: Marzolf (1963), in a laboratory study, found that Pontoporeia selected sediment particle sizes smaller than 0.50 mm in diameter but did not discriminate between smaller sizes. Sand is composed of particles ranging from 1.0 mm to 0.062 mm in diameter, silt from 0.062 to 0.0039 mm, and clay less than 0.0039 mm.

Examination of the percent organic carbon content of the sediment in the present study revealed that Lake Michigan sand has an average carbon percentage of 0.14 with a range of 0.04 to 0.22, sandy silt an average of 0.47 with a range of 0.26 to 0.71, silt an average value of 2.82 with a range of 1.70 to 4.02, and the upper stratum of layered sediment an average value of 1.08 with a range of 0.68 to 1.69. These ranges of percent organic carbon indicate that the largest values of sandy silt overlap with the lowest values of layered sediment, and the largest values of layered sediment overlap with the lowest values of silt.

Marzolf (1963) concluded from laboratory experiments that the selection of a substrate by Pontoporeia was significant only when organic matter was present as a surface film on the sediments. He also found a significant association between the density of this amphipod and sedimentary bacterial numbers and the amount of organic matter in the sediments. Zobell and Feltham (1942) showed that certain species of bacteria are capable of degrading cellulose, chitin, and lignin which most animals find difficult, if not impossible, to digest. They earlier (Zobell and

Feltham 1938) established that a variety of marine organisms can utilize bacteria as an energy source. Baier (1935) suggested that most detritus feeders are nourished by the bacteria which decompose the detritus rather than by the detritus upon which they appear to be feeding. Marzolf found that in the laboratory _Pontoporeia_ actively selected the sediments that had been "conditioned" by the growth of bacteria.

The gut contents of several _Pontoporeia_ collected from the lake and of several maintained in the laboratory were examined in the present study. Aliquots of cultured algae were added weekly to the aquaria of the laboratory reared amphipods. The foregut of the lake samples contained sediments coated with a layer of organic material and an occassional diatom frustule, while the hindgut contained only sediment and diatom frustules. The foregut of the laboratory reared amphipods contained sediment coated with organic matter and intact algal cells. The hindgut contained only the sediments and intact algal cells. While the organic matter on the sediment appeared to be digested, the cellulose walls of the algal cells appeared to be little affected by the passage through the digestive system.

Stepwise Multiple Regression Analysis of the Environmental Parameters

Perhaps the greatest single problem confronting the analysis of a biological system is the confounding effects that can occur between environmental parameters. Within Lake Michigan, depth is ultimately related to all the physical parameters measured (with day of year being

the exception). In the two dimensional presentation of data, such as *Pontoporeia* density versus distance from shore, it is impossible to determine how much of the apparent relationship is actually attributable to depth, bottom type or other environmental parameters. Multiple linear regression is a useful statistical tool in the study of biological systems because it has the ability of mathematically removing the effects of confounding environmental factors.

A remarkable aspect of the multiple regression analysis was the high multiple correlation coefficients that were obtained at the four depth zones: 0.756 for 10-35 m, 0.599 for 36-65 m, 0.677 for 66-105 m, and 0.826 for greater than 105 m. The high multiple correlation coefficients imply that the physical and biological parameters "explain" a large proportion of the changes in amphipod counts.

Within the 10-35 m depth region of the lake, the multiple regression equation showed a significant interaction of depth, sediment type, and distance from shore which indicated that inshore regions of the lake present an unsuitable environment for *Pontoporeia*. The turbulence attributable to waves and water currents of this region have the ability of resuspending and redepositing the finer sediments and detritus into other areas that are less mixed. These shallow areas contain surficial sediments of coarse beach sand and hard bottom types, and fewer amphipods are found there.

The necessity of including the depth squared term in the multiple

regression equation indicated that the relationship between Pontoporeia and depth is not simple or linear. This second order polynomial term probably implies that, in this shallow region of the lake, depth is ultimately associated with the abundance of amphipods, but is also associated to some extent with the other environmental parameters.

At first glance it is surprising that surface temperature should be so important for explaining amphipod abundance in the shallower portions of the lake. Within this area of the lake the thermocline is usually either absent or not well established, so bottom temperature is usually a function of surface temperature. The positive effect of water temperature on the abundance of this amphipod is probably attributable to the effect that temperature has on growth rate. As the amphipods increase in size they are probably better able to survive in this environment.

Beyond 36 m there was little interrelationship between Pontoporeia and the physical environment. At the 36-65 m depth zone, sediment showed the same inverse relationship as it did in the shallower regions and had about the same influence on amphipod abundance. Depth had a slight inverse effect on amphipod counts, and beyond 105 m depth had a very strong negative influence on amphipod density.

Within the deeper portions of the lake the rain of particulate matter is slowed considerably by the water column. Bruun (1957), in an investigation of the ocean, indicated that over great depths this rain of particles, which is mainly derived from plankton, is rapidly consumed by the animals

living at greater depths. Raymont (1963) indicated that although large quantities of organic matter are present in bottom muds, this richness is misleading because the benthos is very much dependent on plankton supply. This is particularly interesting because no association was found between percent carbon in the sediment and the abundance of Pontoporeia.

It is particularly difficult to interpret the significance of the positive statistical associations that occurred between this amphipod and the other macrobenthic groups unless they indicate that the taxonomic groups, and especially the sphaeriids, respond to environmental changes in the same manner as Pontoporeia. The Sphaeriidae were positively associated with Pontoporeia both at the four depth zones and when all depths were combined, while the oligochaetes showed a positive relationship with Pontoporeia beyond 65 m and no apparent association when the lake was treated as a unit. The Chironomidae showed a positive association with this amphipod only at the 66-105 m depth zone. However, the chironomids did show a positive relationship when all depths were combined.

Robertson (1967) reported that 12 species of the Sphaeriidae were found at our sampling stations. Eight of these species, Sphaerium striatinum form acuminatum, Pisidium casertanum, P. compressum, P. nitidum form pauperculum, P. fallax, P. henslowanum, P. idahoense, and P. amnicum occurred between 10 and 20 m. Pisidium lilljeborgi and

S. corneum were found at 10 to 50 m while Sphaerium nitidum occurred between a depth of 20-30 m. Pisidium conventus was found at depths that ranged from 30 to 200 m.

Hiltunen (1967), in an investigation of the oligochaetes of Lake Michigan, found 26 species of Tubificidae, 12 species of Niadidae, and 1 species of Lumbriculidae in three regions of the lake. The areas were located in Green Bay, the southern end of the lake and Ludington harbor. In the southern part of the lake practically all naidids were collected at depths that ranged from 5 to 20 m with a few individuals of Vejdouskyella intermedia being found as deep as 37 m. Members of the families Lumbriculidae and Tubificidae were found at all sampling depths (5-74 m) in the southern areas of the lake.

G. R. Brenniman, J. A. Soyak, and L. L. Curry[2] have examined the depth distribution of the Chironomidae in Lake Michigan. They identified 38 species of midge larvae in the lake with three species, Cryptochironomus digitatus, Procladius adumbratus, and Prodiamesa (Monodiamesa) bathyphila being found throughout the lake. The species of genus Hydrobaenus are found only in the profundal regions of the lake, while larval forms of Tendipis plumosus, T. attenuatus, and T. riparius are found in the shallower near shore and harbor areas.

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[2] Distribution of Midge larvae (Tendipedidae: Diptera) in Lake Michigan. Paper presented at the 9th Conference on Great Lakes Research. Chicago, Ill., 1966.

It can be seen, then, that the macrobenthic groups associated with Pontoporeia represent a composite of several species. Each species has behavioral characteristics and environmental requirements that are unique for its niche. These positive associations, as was indicated earlier, may merely reflect the fact that the larger sampling areas of the Ponar and Smith-McIntyre benthos samplers mask the patterns of the microassociations and those regions within the lake that are preferred by Pontoporeia are also selected by the other macrobenthis groups.

SEASONAL DISTRIBUTION

During the present study the density of amphipods has been found to change very little over a 24-hour period of time, and there appear to be little changes with time in the average standing crop of amphipods when all stations are combined.

Eggleton (1937) combined the monthly Pontoporeia counts for the samples collected from Lake Michigan in 1931. He found a slight decline in the density from May to June, a marked increase from June to July, a seasonal maximum in August, and a sharp decline in the counts from August to November. Treating his 1932 samples in the same manner he found a reverse trend. The abundance of amphipods declined slightly from April to June, decreased sharply from June to July, and then increased considerably from July to September. He concluded that the dissimilarities which existed between the seasonal samples of the two years reflected the natural tendency of any biological system to vary

from year to year. However, Eggleton had only 167 samples, collected over a two year period, available for his analysis while more than 1,700 samples were collected in the three years of the present study. Further, his 1932 samples were from a different region of the lake than those taken in 1931.

Henson (1954), in an investigation of a single produndal station in Cayuga Lake that was approximately 100 m deep, reported that in 1952 there was a significant increase in the total crop of Pontoporeia occurring from May to October. He found that the 1953 standing crop was significantly greater than that in 1952. He attributed the 1953 increase to the production of young and the immigration of amphipods from the shallower depths.

Although there was no significant seasonal variation in the abundance of amphipods at the 10-35 m zone in Lake Michigan there was considerable variation within sampling seasons. The numerical decrease from March to April 1966 represents the death of spent females. The low density of amphipods in the late spring and early summer is probably attributable to losses arising from the elutriation-screening device that separates the organisms from the sediment. Large numbers of newly released amphipods may have been swept through the separating screen. As the small amphipods increased in size, they were less inclined to be lost in this manner. The remaining three depth zones do not appear to show any well defined patterns within the sampling periods.

It is difficult to interpret the similar patterns of amphipod abundance that occurred at stations C-2 through C-7. Samter and Weltner (1904), Ekman (1913), and Henson (1954) have shown that as smaller oligotrophic lakes warm in the spring and summer, Pontoporeia has a tendency to migrate to the colder hypolimnion. The investigations of Wells (1960) and Marzolf (1963) have shown that larger Pontoporeia are active swimmers and these larger amphipods could possibly represent transient groups that move from area to area. However, a reexamination of the size frequency histograms showed that there appeared to be little exchange of size groups within the shallower waters of the lake. These fluctuations in abundance also did not appear to be the result of reproduction.

It is possible that these changes in abundance were the result of sampling error. The ship logs were examined to determine if the fluctuations in the amphipod counts resulted from samples being taken during periods of high seas. Sampling in rough weather often caused the dredges to close prematurely. There appeared to be no association between the state of the sea at the time the samples were taken and the variation in the amphipod counts. All persons involved in collecting and processing the samples were well trained in the sampling procedures, thus the collecting and processing of the samples should not represent a source of error.

Smith (1968) indicated that adult alewives are densely concentrated

on the bottom in the deepest parts of Lake Michigan in mid-winter where they seek the warmest water of the lake. In late winter and early spring they move shoreward in dense schools, spawn near shore, in rivers, and in bays during the late spring and summer, and begin to migrate back to open waters of the lake in the fall. He feels that when the alewife is concentrated inshore in the summer, the deeper water, previously inhabited by fishes that were replaced by the alewife, are essentially unoccupied and the invertebrate fauna is incompletely utilized. He feels that similar situations occur during other seasons as the alewife moves from zone to zone.

Morsell and Norden (1968) reported that as the length of alewives increased beyond 119 mm they progressively relied more and more on P. affinis as a source of food. They found, by stomach analysis, that Pontoporeia constituted nearly 80 percent of the dry weight for the total stomach content of alewives living in the littoral and sublittoral regions of the lake.

The seasonally discriminant exploitation of Pontoporeia by alewives, as well as amphipod predation by other bottom feeding fishes, could possibly contribute the observed seasonal fluctuations.

PATTERNS OF SPATIAL ABUNDANCE

Powers and Robertson (1965) found the standing crop of Pontoporeia higher in the inshore areas of the northern basin of Lake Michigan than comparably placed stations located in the southern basin. Their results

generally agree with the findings of the present study.

Whenever the effect of depth is statistically removed from the abundance of Pontoporeia, the average density appears to be highest at the most western inshore stations in the northern basin of the lake. Ayers et al. (1958) have shown that areas on the western margin of the lake, in the vicinity of stations E-6 and D-6, are periodically subjected to upwelling and currents sweeping down from Green Bay. The increased productivity attributable to upwelling plus the added nutrients carried south from the Green Bay region could make the western protions of the lake more productive than would normally be expected. The inshore regions of the eastern portions of the lake, in proximity to the C, D, and E transects, are subjected to upwelling caused by short-lived NE winds and the normal outflow current which is enriched by local runoff and nutrients sweeping north from the southern basin. The amphipod density also appears to be higher within these regions.

Station B-8, located approximately 2 miles from Waukegan, Wis., station A-6 situated 9 miles from Chicago, and A-1 located 2 miles from Benton Harbor, Mich., are found within the regions of the southern lake basin that have been classified as grossly polluted by the Federal Water Pollution Control Administration (1968). Although it is currently fashionable to regard areas in the lake with low Pontoporeia densities as areas of gross pollution, it must be pointed out that the sediment types in these regions are quite variable, ranging from fine beach sands to glacial tills,

and these shallow areas are subjected to considerable turbulence during periods of intense storms. While there is considerable truth to the fact that these regions have been subjected to pollution, they are probably natural regions of low amphipod productivity.

CONCLUSIONS

This amphipod, *Pontoporeia affinis*, is a remarkable organism. The field observations of this study indicate that *Pontoporeia* is capable of enduring a wide range of environmental conditions. In Lake Michigan, it is found from the sublittoral to the deepest profundal areas and tolerates water temperatures that range from 1° to 19° centigrade. Although *Pontoporeia* is a burrowing amphipod it is also found, in low densities, within hard bottom surficial sediments. Juday and Birge (1927), in an investigation of Green Lake, Wis., found that *Pontoporeia* was able to survive within the sediments when the water contained 0.72 cc/l dissolved oxygen one meter above the bottom.

The results of this study strongly indicate that Lake Michigan cannot be treated as a unit in the analysis of the interrelationships of *Pontoporeia* and its environment. This amphipod has the extraordinary capability of adjusting to the ambient environmental conditions and has even adapted its reproductive cycles to comply with these local conditions.

Within the sublittoral regions of the lake, *Pontoporeia* has developed two distinct reproductive patterns that appear to be related to the water temperature. It matures in one year in the warm shallow inshore regions of the sublittoral and requires two years to mature in the deeper portions of this zone. *Pontoporeia* of the sublittoral are geared for a late winter-

early spring period for reproduction; in other depth zones they breed year round.

The greatest environmental stresses for Pontoporeia also occur within the sublittoral. Later visits to the sublittoral short-term study area (in August and November) showed that molar action attributable to storms and bottom currents had caused considerable shifting of the bottom sediments and had resuspended the detrital material. The greater variability in the amphipod counts of the sublittoral zone found throughout our studies probably reflects the disrupting forces attributable to ambient meteorological and limnological conditions and to the general environmental heterogeneity of this region.

Pontoporeia reaches its maximum density at the junction of the sublittoral and profundal zones. This region corresponds roughly to the lower limit of the thermocline. The surficial sediments within this area are little affected by turbulence, and the range of bottom temperatures is not so extreme as in the shallower inshore waters. In this area and the adjacent profundal zone, Pontoporeia matures and breeds intermittently throughout the year. There appears to be a greater proportion of breeding females in the amphipod population that inhabits this area and the contiguous profundal areas.

The junction of the sublittoral and profundal zones represents a reasonably stable environment where Pontoporeia can effectively utilize the rain of suspended particulate matter that is created through the enrich-

ment by upwelling, local runoff, and also by the dominant along shore current. It must be emphasized that this junction changes with the seasons, and its location within an area is dependent on the morphometric features of the lake and the prevailing meteorological conditions.

The profundal zone represents the most stable environment of the lake with all areas of the profundal sharing a common low water temperature. The Pontoporeia of this region probably require three or more years to mature, and although breeding is intermittent throughout the year only a very small portion of the population appears to be mature at any particular time. The density of Pontoporeia in this zone shows a strong inverse relationship with depth, which most likely reflects the negative effect that depth has on the rain of suspended particulate matter. The lack of available nutrients is probably the most restrictive element of the profundal environment.

As Pontoporeia is the only macrobenthic invertebrate that is ubiquitously distributed throughout the sublittoral and profundal zones of the lake, it should play an increasingly important role as an indicator of water pollution. Cook and Powers (1964) showed that a benthic community subjected to the effluent of the St. Joseph River contained few Pontoporeia and an abundance of oligochaetes. On the other hand, a benthic community adjacent to Little Sable Point, which has no major tributaries, contained a large population of Pontoporeia and few oligochaetes. Ayers and Huang (1967) included macrobenthic sampling in a pollution study of

Milwaukee Harbor and the adjacent embayment. Inside the breakwater they found a high density of oligochaetes, no amphipods, and considerable environmental degradation. The embayment immediately outside the breakwaters also showed environmental degradation, high densities of oligochaetes, and occasionally Pontoporeia.

The low density Pontoporeia, as a criterion for water pollution, is very unsatisfactory because the abundance of this amphipod is dependent on many environmental conditions, some of which bear no relation to water pollution. This study showed that bottom sediments can strongly affect the density of Pontoporeia. High water temperatures and low oxygen tensions, which were previously considered limiting environmental factors for this amphipod, are not necessarily a deterrent for their habitation. Before an area can be classified as polluted, by using the low levels of Pontoporeia as the indicator of pollution, a very careful examination must be made of the environment to determine if low densities are attributable to pollution or the disrupting effects of an environmental factor.

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